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Classification, phylogeny and zoogeography of the world species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae)

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Classification, phylogeny and zoogeography of the world species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae) submitted by R.E. Roughley in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Abstract

Twenty-six species and two subspecies comprising the world fauna of *Dytiscus* Linnaeus are keyed, redefined, characterized and illustrated. Arrangement of *Dytiscus* into subgenera is unwarranted based on the phylogenetic analysis presented. Taxonomic changes include recognition of *D. carolinus* Aubé 1838; synonymy of *D. validus* Régimbart 1899 (=*D. sharpi* Wencke 1875); use of *D. czerskii* Zaitsev 1953 at subspecific level for eastern Palearctic specimens within *D. marginalis* Linnaeus 1758 (western Palearctic specimens); arrangement of *D. lapponicus* Gyllenhal 1808 into two subspecies, the nominate, widespread Palearctic form, and *D. lapponicus disjunctus* Camerano 1880 from the European Alps; and synonymy of *D. piceatus* Sharp 1882 (=*D. latro* Sharp 1882). Nearctic records of *D. marginalis* refer to *D. cordieri* Aubé 1838. Even though types were not seen, the names *D. albionicus* and *D. fuscostriatus*, both of Motschulsky 1859, are transferred to synonymy with *D. marginicollis* LeConte 1845. Lectotype designations are provided for the following: *D. sharpi* Wehncke 1875 (male in MNHN, labelled: Japonia); *D. validus* Régimbart 1899 (=*D. sharpi* Wehnke 1875) (male in MNHN, labelled: Nagahama); *D. pisanus* LaPorte Compte de Castelnau 1835 (male in BMNH labelled: Italia); *D. submarginalis* Stephens 1828 (=*D. marginalis* Linnaeus 1758) (male in BMNH, without locality data); *D. angustatus* Stephens 1828 (=*D. circumcinctus* Ahrens 1811) (male in BMNH, without

locality data); *D. parvulus* Motschulsky 1852 (=*D. alaskanus* J. Balfour-Browne 1944) (male in UMHF, labelled: Kadjak); and *D. dauricus* Gebler 1832 (male in MNHN, labelled: Sib.or. 62).

Information concerning holotypes is as follows: *D. marginicollis* LeConte 1851 (female in MCZC, labelled with green circular label: Type 6091); *D. hatchi* Wallis 1950 (male in CNIC, labelled: Pond N. of Bethel, Washington, Apr.21, 1940); *D. sublimbatus* LeConte 1857 (=*D. cordieri* Aubé 1838) (female in MCZC, labelled: Or.); *D. pisanus* var. *nonsulcatus* Zimmermann 1919 (in ZSBS, labelled: Tanger); *D. persicus* Wehncke 1876 (female in MNHN, labelled: Persia, settente.); *D. latro* Sharp 1882 (female in BMNH labelled: Manchuria); *D. piceatus* Sharp 1882 (=*D. latro* Sharp 1882) (male in BMNH labelled: Irkutsk, Siberia); *D. stadleri* Gschwendtner 1938 (=*D. latro* Sharp 1882) (male in ZSBS, labelled: [indistinguishable writing, ?=Berisovka]); and *D. sinensis* Feng 1935 (male in USNM, labelled: Szechuen, CHINA, D.C.Graham; Yin-Kuan-Tsai, 12,300 ft., vii.21.30);

Treatment of each taxon includes, when appropriate: synonymic list with information about type locality and label information from types examined, derivation of epithet, notes about type material, diagnostic combination, description in tabular form, taxonomic notes, discussion of variation, discussion of natural history, general description of distribution as well as map of localities, chorological and phylogenetic relationships. In addition,

line drawings of dorsal view of adults, coloration of pterothoracic and abdominal sterna, metacoxal processes and trochanter shape are provided. Views of dorsal, ventral and lateral aspect of the median lobe of adult males are represented by scanning electron micrographs.

Cladistic analysis shows that the sister group of Holarctic *Dytiscus* is the Australian genus *Hyderodes*. Ancestral Dytiscinae probably arose in southern Gondwanaland or Pangaea, with the separation of African and Australian plates providing vicariant separation of ancestral stocks of these genera. Mountain ranges have existed along the southern edge of Gondwanaland since the Upper Jurassic. Although these mountains provided a corridor to terrestrial fauna and stream inhabitants, they probably formed a barrier to taxa adapted to deciduous forest ponds – the habitat of original as well as plesiotypic, extant Dytiscini. Ancestral *Dytiscus* dispersed northward through Africa along a temperate forest corridor to reach Laurasia. Subsequently, *Dytiscus* became extinct in the Afrotropical region.

Ancestors of at least two plesiotypic clades, *D. verticalis* species-group (monobasic), and *D. hybridus* species-group (*D. harrisii* Kirby, *D. hybridus* Aubé, *D. marginicollis* LeConte and *D. habilis* Say), were present on Laurasia prior to its breakup into North America and Eurasia, even though both lineages are now exclusively Nearctic. A zoogeographic treatment of these species-groups incorporates ecological, chorological and phylogenetic

information. Two co-occurring species, *D. hybridus* and *D. verticalis*, occupy ancestral habitats, but differ markedly in body size (possibly arising vicariantly with character displacement allowing habitat partitioning). Another species, *D. harrisii*, occupies the same range, but prefers more lotic habitats (possibly representing sympatric speciation by habitat specialization). The other two species, western *D. marginicollis* and Mexican *D. habilis* have ranges which do not overlap that of their closest relative, and are probably derived by vicariant speciation events.

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I express my sincere appreciation to my supervisor, Dr. G.E. Ball for his help and advice during my study. His constant enthusiasm and insight as well as attitude toward teaching and research are of great value. The climate of learning which he has helped create among the faculty and staff of the department has made the opportunity to study and conduct research there a very beneficial experience.

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To my colleagues in the department I owe a great deal. They have been most helpful in discussions of specific problems and of general theory and application of systematics, as well as providing many specimens of *Dytiscus* or other information. I thank them all, but certain of them deserve special mention for their detailed contributions. These are Drs. Ron Aiken, Steve Ashe, Art Borkent, Henri Goulet, Dave Kavanaugh, Don Lafontaine, Fran Leggett, Andy Nimmo and John Spence, as well as John Acorn, Bob Anderson, Jeff Cumming, Doug Currie, Henry Frania, Gary Gibson, Jean-François Landry, Eric Maw, Jim O'Hara, Kate Shaw and Felix Sperling.

As explained elsewhere, examination of specimens of *Dytiscus* involved visiting collections, and I express my appreciation to the respective curators for their assistance during my visit to their institutions.

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1. Introduction

The Zoological Institute of Marburg, Germany must have been an exciting place for study of dytiscids during the late 19th and early 20th century. Professor E. Korschelt was in charge of a battery of students whose general project was intensive and careful investigations of all aspects of taxonomy, natural history, structure, function, *etc.* of *Dytiscus*. This group concentrated on one of the larger, most commonly available species, *Dytiscus marginalis* L. Their collective efforts culminated in a magnificent two volume work of more than 1800 pages edited by Korschelt (1923, 1924). Some, but not all, chapters of this work had been published elsewhere by the contributing authors. This work and subsequent contributions by both these and other workers must make *D. marginalis* at least the most studied member of Adephaga and possibly one of the most studied beetles.

The genus *Dytiscus* is one of the 25 genera originally recognized as comprising the Coleoptera by Linnaeus (1758:342). The Linnaean definition of *Dytiscus* was based primarily on presence of natatory setae on the posterior legs, and as such it contained beetles now assigned to Hydophiloidea and Dryopoidea as well as Dytiscoidea. Of the fifteen taxa assigned to *Dytiscus* by Linnaeus, only two (*D. latissimus* and *D. marginalis*) are accepted within the present definition of the genus, established by Erichson (1832)

Even the correct spelling and meaning of the generic epithet has engendered controversy. According to Blunck

(1913:8) and J. Balfour-Browne (1960), Geoffroy (1762:185) was probably the first author to note that *Dytiscus* was an incorrect transliteration of the Greek word for 'diver'. Many authors subsequently used the emended "*Dyticus*" or "*Diticus*", although Schmeidlin (1786:239) suggested that Linnaeus' spelling may be derived from the word 'disci' referring to the form of the male protarsus of specimens of *Dytiscus* (Blunck 1913:9). This would appear unlikely given the composition of the genus by Linnaeus. The present spelling of the generic name was established as valid in 1961 by Opinion 619, Bulletin of Zoological Nomenclature 18.

Blunck (1913:2-30) discusses the early, including pre-Linnean, taxonomic history of *Dytiscus*. Blunck's treatment is exceptionally thorough and is invaluable as a source for, and interpretation of, the early treatises which treat various species of *Dytiscus*, but perhaps more importantly, he has allowed entrance into philosophical and interpretive aspects of the work of these early systematists. This is particularly useful because of the nomenclatural problems such as those created by the treatment of dimorphic adult females (elytron either sulcate or non-sulcate). Perhaps no other feature of *Dytiscus* has led to the proliferation of names, long and sometimes heated discussions of nomenclature in the literature, as well as loss of time from more important taxonomic endeavours, as has that created by the occurrence of two states of female elytra. The two forms of any given European species were consistently provided with separate specific level epithets. Subsequent demonstration of the dimorphic nature of this variation has led to retention and demotion of these names to the level of variety and abberration. Use of such names in one taxon has precipitated creation of corresponding names in other taxa, which has in turn brought about debate of proper assignment of varietal names, concluding in further confusion and nomenclatural difficulties.

One hundred years have passed since the world fauna of *Dytiscus* was last described and compared by David Sharp (1882). Previous to this, the only comprehensive analysis of the burgeoning knowledge of the world fauna had been that of Charles Aubé in 1838. Both monographs included much new knowledge about adult Hydradephaga in general, and about members of *Dytiscus* in particular. Many of the characters used in the present classification of these groups were first presented in these works. These books, in my opinion, represent two of the most outstanding studies of classification of Hydradephaga. Quality and importance of such works is dependent upon two factors: ability of the taxonomist and quality and diversity of specimens available. The high degree of ability of both these workers is evident from, and has been tested by, the continuing importance of these publications. Almost as important are the collections with which these men worked. Aubé and Sharp had the advantage of extensive, worldwide collections accumulated within Europe during the 18th and 19th centuries.

Since 1882, additional names and synonymies have been proposed, and many new distributional records acquired. Because of the amount of information available concerning various members of *Dytiscus*, even knowledgeable coleopterists have assumed that this genus was well understood taxonomically. However, those who have attempted to identify specimens of *Dytiscus* to species (from areas outside Europe) discovered that this was difficult to accomplish. Reference to such recent works as Wallis (1950), Zaitsev (1953:341-354), Pederzani (1971) and Larson (1975:394-405) demonstrated that there was no lack of distinctive character states in external features and male genitalia, yet showed that type material of some species was inadequately understood and generally made it apparent that much still remained to be discovered about classification of the species of this genus. More specifically, they revealed that an adequate revision would have to be based on a world-wide study.

Achievement of the means to easily and accurately identify specimens of species is only the first step in gaining understanding of a genus. Additional steps which taxonomists ought to take are analyses of any further information that they have available concerning the members of the genus (*i.e.* holomorphological, chorological, paleontological and parasitological - Hennig 1966) and integration of this into an appreciation of evolutionary aspects of the taxon under study. Unfortunately, the amount of the latter two types of information are severly limited for *Dytiscus*.

This revision offers means of identification of adults, information about type specimens, and a synopsis of natural history and geographic distribution of species of *Dytiscus*. These data provide the basis for phylogenetic and zoogeographic analyses. Much information concerning other life stages has been gathered or is available elsewhere, but remains to be analyzed. Later integration of this information will test the relationships proposed here.

2. Materials and Methods

2.1 Materials

This revision is based on study of 13,300 adult specimens of *Dytiscus*, either borrowed or personally collected. The following alphabetically arranged acronyms represent collections from which specimens were borrowed. Names of respective curators are also presented. In this list, private collections have the person's name placed first, after the acronym. For institutional collections, the curator's name is placed last. My collection is included in the material denoted UASM.

AMNH – American Museum of Natural History, Central Park W. at 79th St., New York, New York 10024; L.H. Herman, Jr.

ANIC – Australian National Insect Collection, C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T. 2601, Australia; J.F. Lawrence.

ANSP – Academy of Natural Sciences, 19th and Parkway, Philadelphia, Pennsylvania 19103; S.S. Roback.

ANSU – A.N. Nilsson, Department of Biology, Section of Ecological Zoology, University of Umeå, S-901 87 Umeå, Sweden.

BMNH – Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD; M.E. Bacchus and P.M. Hammond.

BYUC – Department of Zoology and Entomology, Brigham Young University, Provo, Utah 84601; S.L. Wood.

CARR – Mr. and Mrs. J.L. Carr, #24 Dalrymple Green NW, Calgary, Alberta T3A 1Y2.

CASC – Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; D.H. Kavanaugh.

CISC – Division of Entomology and Parasitology, Agricultural Experiment Station, College of Agricultural Sciences, Univeristy of California-Berkeley, Berkeley, California 94720; J.A. Chemsak.

CNIC – Coleoptera Section, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario K1A 0C6; A. Smetana.

CUCC – Department of Entomology and Economic Zoology, Clemson University, Clemson, South Carolina 29631; S.B. Hays.

CUIC – Comstock Hall, Department of Entomology, Ithaca, New York 14853; L.L. Pechuman.

DEFW – Department of Entomology, Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota 55101; P.J. Clausen.

EMUS – Entomological Museum, Department of Biology, Utah State University, Logan, Utah 84322; W.J. Hanson.

ENMV – Entomologie, Naturhistorisches Museum, Burgring 7, A – 1014 Vienna, Austria; F. Janczyk.

FMNH – Division of Insects, Field Museum of Natural History, Roosevelt Road at Lakeshore Drive, Chicago, Illinois 60605; E.H. Smith.

FNYC – Department of Zoology, Indiana University, Bloomington, Indiana 47401; F.N. Young.

GWSC – G. Swenson, Department of Biology, Ithaca College, Ithaca, New York 14850.

GWVA – G. Wewalka, Kandlgasse 19-21, 1070 Vienna, Austria.

GWWC – G.W. Wolfe, Department of Entomology and Economic Zoology, Rutgers University, New Brunswick, New Jersey 08903.

HBLC – H.B. Leech, 1435 Howell Mountain Road North, Angwin, California 94508.

HNHM – Hungarian Natural History Museum, Baross utca 13, H – 1088 Budapest, Hungary; Z. Kaszab.

ICCM – Section of Insects and Spiders, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213; G.E. Wallace.

INHS – Natural Resources Building, Illinois Natural History Survey, Urbana, Illinois 61801; W.U. Brigham.

LACM – Department of Entomology, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007; C.L. Hogue.

MCZC – Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; M. Thayer.

MNHN – Entomologie, Muséum Nationale d'Histoire Naturelle, 45 bis, Rue de Buffon, Paris (Ve), France; H. Perrin and J.J. Menier.

MSUC – Department of Entomology, Michigan State University, East Lansing, Michigan 48824; R. Fisher.

MUIC – Department of Biology, Memorial University, Saint John's, Newfoundland A1B 3X9; D.J. Larson.

NDSU – Department of Entomology, North Dakota State University, Fargo, North Dakota 58102; E.U. Balsbaugh, Jr.

NMSU – Department of Biology, New Mexico State University, Las Cruces, New Mexico 88001; J.R. Zimmerman.

ODUC – Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23508; J.F. Matta.

OSUC – Department of Entomology and Zoology, Collection of Spiders and Insects, Ohio State University, Columbus, Ohio 43210; C.A. Triplehorn.

OSUO – Department of Entomology, Oregon State University, Corvallis, Oregon 97331; J. Lattin.

PMNH – Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; C.L. Remington.

RHTC – R.H. Turnbow, Jr., Department of Entomology, University of Georgia, Athens, Georgia 30602.

ROMC – Department of Entomology and Invertebrate Zoology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6; G.B. Wiggins.

SCSU – Department of Biological Sciences, St. Cloud State University, St. Cloud, Minnesota 56301; R.D. Gundersen.

SDMC – Entomology Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112; K. Faulkner.

SDSU – Entomology-Zoology Department, College of Agriculture and Biological Sciences, South Dakota State University, Brookings, South Dakota 57006; B. McDaniel.

SMNS – Entomologie, Staatliches Museum für Naturkunde Stuttgart, 7140 Ludwigsburg, Arsenalplatz 3, West Germany; K.W. Harde.

SPMC – Saskatchewan Museum of Natural History, Wascana Park, Regina, Saskatchewan S4P 3V7; R.R. Hooper.

TAMU – Department of Entomology, College of Agriculture, Texas A & M University, College Station, Texas 77843; H.R. Burke and S.J. Merritt.

UAIC – Department of Entomology, University of Arizona, Tucson, Arizona 85721; F.G. Werner.

UANH – Department of Zoology-Entomology, Auburn University, Auburn, Alabama 36830; G.W. Folkerts.

UASM – Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.

UBCZ – Spencer Entomological Museum, Department of Zoology, University of British Columbia, 2075 Westbrook Place, Vancouver, British Columbia V6T 1W5; G.G.E. Scudder.

UCEC – University of Colorado Museum, Department of Entomology, University of Colorado, Boulder, Colorado 80309; U.N. Lanham.

UCIC – Department of Biology, University of Calgary, Calgary, Alberta T2N 1N4; G. Pritchard.

UCRC – UCR Entomological Collection, Department of Entomology, University of California-Riverside, Riverside, California 92502; S.I. Frommer.

UCSE – Biological Sciences Group, Museum of Natural History, University of Connecticut, Storrs, Connecticut 06268; P.W. Severance and C.S. Henry.

UGIC – Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1; D.H. Pengelly.

UMBS – University of Michigan Biological Station, Pellston, Michigan 49769; E.M. Barrows.

UMHF – Division of Entomology, Zoology Museum, University of Helsinki, N. Järnvägsgatan 13, SF-00100 Helsinki 10, Finland; H. Silfverberg and A. Jansson.

UMMZ – Division of Insects, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104; R.D. Alexander.

UMRM – Entomology Research Museum, 1-87 Agriculture Building, University of Missouri, Columbia, Missouri 65201; W.R. Enns.

USNM – Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; P.J. Spangler.

UVCC – Marsh Life Science Building, Department of Zoology, University of Vermont, Burlington, Vermont 05401; R.T. Bell.

UWEM – Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706; W.E. Hilsenhoff.

WLHC – W.E. Hilsenhoff, Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706.

WUBC – W.U. Brigham, Natural Resources Building, Illinois Natural History Survey, Urbana, Illinois 61801.

ZMLS–Zoological Institute, University of Lund, S-223 62 Lund, Sweden; P. Brinck and S. Arlebo.

ZSBS – Entomologie, Zoologisches Sammlung des Bayerischen Staates, 8000 Munich 19, West Germany; G. Scherer.

2.2 Methods and Techniques

2.2.1 Cleaning and dissection of specimens

Many specimens of *Dytiscus* are greasy and dirty, and, as such, they are not useful for detailed examination of structural features. Specimens were cleaned by placing them in a beaker of warm water to which was added a small amount of ammonia-enriched detergent. The beaker was placed on a hot plate adjusted to low heat for about 12 hours. After removal, specimens were rinsed with clean water and appendages positioned to avoid possibility of breakage.

Dissection of genitalia preceded the clean-water rinse. A number of techniques for extracting the sclerotized terminalia of adult *Dytiscus* were tried. The most effective method for male specimens is to grasp the relaxed beetle in one hand and to deflex the abdomen. An incision made between the third and fourth terga allows the base of the median lobe and parameres to be grasped with a pair of fine forceps. By pulling anteriorly and then upward and posteriorly, the median lobe and parameres of most specimens can be extracted without damage and the remainder of the aedoeagus left in place. Removal of the male genitalic capsule by grasping the apex of the median lobe, parameres or associated structures is to be avoided because of the probability of damage. The median lobe is best separated from the parameres by placing two pairs of forceps into the basal space provided by the curvature of the median lobe and then gently pulling the forceps in opposite directions. This technique pulls the base of the median lobe away from the bases of the parameres and allows for clean preparation with a minimum of damage.

Terminalia of adult female specimens were dissected in a different manner. Musculature around an ovipositor was cut with a lancet inserted through the abdominal apex and then the capsule pulled out with forceps. Because stylomere I, at rest, is flexed anteriorly over the top of the remainder of the capsule there is little possibility of damage using this technique. Preliminary analysis of shape of the apex of stylomere I (*e.g.* Pederzani 1971: 221) indicates that this feature may be taxonomically useful. However, the distinction among taxa is difficult to characterize and was not used in this study.

Portions of both male and female genitalic capsules removed from specimens were glued to cards placed on the pin of the specimens from which they were removed. Teneral or unsclerotized genitalia were placed in small, glycerine-filled vials and mounted on the specimen pin.

2.2.2 Measurements

Adult specimens of *Dytiscus* were measured for total length (TL) and greatest width (GW) of the body. A ratio of these values (TL/GW) gives an index of body shape. Measurements were taken by means of a moveable stage Vernier scale to which a specimen holder was attached. By lining up a set of cross-hairs in the microscope eyepiece with an end of the beetle and then turning the knob on the stage micrometer until the other end of the specimen was lined up with the cross-hairs, the numerical value could be read from the scale on the stage micrometer.

An investigation of the value of absolute size measurements of specimens of *Dytiscus* and its taxonomic value was initiated after noting discrepancies in overall size of specimens. For instance, Larson (1975:397) commented on the smaller mean TL of adult specimens of *D. harrisii* from Alberta and the Northwest Territories compared to specimens from Ontario and Wisconsin. I found a similar but less striking difference: average TL for 10 specimens from Alaska, Alberta, Northwest and Yukon Territories was 34.9 mm, compared to 36.8 mm for 10 specimens from Ontario. Three adult male specimens of *D. harrisii* which I collected by bottle traps near Old Crow, Yukon Territory, however, had an average TL of 36.6 mm. In addition, a single male collected as a prepupa from Kneehills Creek near Acme, Alberta is 39 mm long. This suggests a sampling bias, although there was no significant difference, possibly due to the male-dominated samples (male specimens are commonly slightly larger than females).

Another taxon, *D. dauricus*, which is more common in Alberta, was more intensively investigated for average specimen size with respect to method of capture. The results are presented in Table 1. Similar trends were found in most species for which I have sufficient numbers of bottle-trapped specimens.

Adults of larger species of dytiscids are very quick and agile swimmers. This was superbly demonstrated to me by a collecting experience in a southern Alabama swamp on a hot day in May, 1978. Specimens of either *D. carolinus* or *Cybister* sp. were frequently surfacing to renew their respiratory air bubble, their location marked by tips of elytra at the water surface. More than 20 attempts to collect these beetles, whose location could be pin-pointed, with a dip net failed to yield a single adult specimen. Similarly, at George Lake near Busby, Alberta, hours of dip net collecting can yield only a few specimens, whereas bottle traps have yielded in excess of 80 specimens (R.B. Aiken, pers. comm.).

Adults of smaller species of dytiscids are more commonly and easily collected with a dip net. This same phenomenon could be true for specimens of a single species of *Dytiscus* – *i.e.* smaller specimens have a greater chance of being caught by dip netting. Differences in TL for adult *Dytiscus* noted above are probably correlated with the method of capture.

Due to this sampling bias, I have excluded body measurements of population samples of species of *Dytiscus* from the descriptions of the species. I present only the extremes of measurements of TL, GW and TL/GW for each taxon, and only as an indication of size range (Table 2). These measurements are based on specimens examined.

2.2.3 Taxonomic Procedure

There are logistic problems associated with a taxonomic revision of large specimens and part of the procedure used to overcome these are presented under the section on Materials. Travel to museums for the purpose of identifying and obtaining data from specimens differs from normal taxonomic procedure in entomology. Instead, I attempted to learn the characteristics and limits of species before leaving for museum travel. This was done by intensive study of representatives of each species and by reference to important faunistic treatments such as Larson (1975) for Nearctic species, and F. Balfour-Browne (1950), Zaitsev (1953) and Schaeflein (1971) for Palearctic taxa. In addition, other publications of smaller scope were used to allow interpolation of other taxa treated in these sources.

Most specimens were examined, determined, and labelled, and label information recorded from them while within the museums visited. A problem with this approach is that assignment of specimens to a particular name is done comparatively quickly, with little opportunity for re-examination. Therefore, there is a pronounced possibility of misdetermination of specimens. In an endeavour to reduce such errors, problematic specimens were borrowed from museums and studied in a manner similar to that described by Erwin (1970:9-10) and Whitehead (1972:140-141).

2.2.4 Descriptive Format

The treatment of each taxon begins with reference to the original description of each valid name or synonym of that taxon. This is followed by information about type locality and information about label data from, and repository of, type material, if known. Most species of *Dytiscus* have a long taxonomic history. Instead of citing all references, the above information is followed by reference to Zimmermann's (1920) thorough catalogue, which provides reference to most, if not all, pre-1920 workers of importance. Any citations of a name after 1920 follow the Zimmermann reference in chronological order, but citations of other catalogue or faunal lists are omitted.

For the valid name of each taxon, I have provided an explanation of the meaning of the name. If further explanation is needed for the status or location of type specimens, this follows the etymological section. A diagnostic combination provides a list of characteristics useful for identification of adult specimens.

Descriptions of species are provided by reference to Table 3. A tabular method of description is of great value because of reduced length and increased ease of comparison. Construction of this table follows the general format presented by Erwin (1982) except that the characters are arranged in phylogenetic sequence – *i.e.* the first character state of each character discussed is plesiotypic while the second is apotypic. For explanation of the rationale of character state assignment see Section 4.3.1. The description also contains reference to figures of structural features provided for each taxon.

Treatment of variation in structural features is confined to taxonomically important characters, regional differences in number of females with grooved elytra, and geographically related trends of other features. In the section on natural history, I attempt to provide information about the habitat or habitats of occurrence and some life history features for adults of *Dytiscus*. These sections are generally more extensive for Nearctic species for which I have field and laboratory observations. For most Palearctic species, I present a summary of the information presented in selected references, or provide reference to more extensive works.

Distribution is shown on maps (see Distribution Maps section below for explanation of procedures used to make up the maps) and this information is generalized into a description of the range. A section entitled chorological relationships provides information about geographic co-occurrence with other species of the genus.

Many Palearctic species of *Dytiscus* have their closest relatives in the Palearctic region, while other species of either realm are members of a small clade restricted to that realm. The relative phylogenetic position of each taxon is presented in a discussion of phylogenetic relationships. A total of the number of specimens examined as well as the number of each sex is the final entry of each species treatment.

2.3 Illustrations

2.3.1 Illustrations other than distributional maps

Line drawings were made with the aid of a camera lucida mounted on a Leitz steroscopic microscope. Illustrations of median lobes of males of various taxa of *Dytiscus* were made by mounting these structures on stubs, onto which was placed two-sided tape, coating with gold and photographing with the a scanning electron microscope, Cambridge Stereoscan 5150. Subsequently median lobes were removed from the stubs and placed back on the genitalia card of the specimen from which they originated.

2.3.2 Distribution maps

2.3.2.1 Mapping of specimen localities

Standard techniques were used for mapping specimen localities and consisted of finding a locality, usually in an atlas (but see below), and placing a symbol on the approximate locality on an outline map and within the region indicated (*e.g.* province, state, départemente, kraj, *etc.*). Within the Nearctic region, this process was straightforward and did not present many problems. All Nearctic locality records are based on specimens seen during this study or by

Larson (1975). All Nearctic locality records and all Palearctic records for which specimens were examined are indicated by filled symbols (*e.g.* •).

Because of logistic problems explained elsewhere, I have accepted some literature records that I could not verify for some Palearctic species of *Dytiscus*. This was done because it was determined that the historical assignment of most Palearctic taxa was in agreement with, or could be assigned to, my concepts of these taxa. Also, examination of collections within selected European museums convinced me that the degree of accuracy of assignment of most Palearctic taxa was quite high. Principally because of consistency, literature records were accepted as useful and accurate additions to knowledge of distribution of these taxa. I believe that amount of error introduced is insignificant compared to amount of information that would be lost by exclusion of literature records. Literature records for localities are also indicated by filled symbols (*e.g.* •).

For the most part, literature records for political areas in which a specific locality is not mentioned were ignored. An exception to this is locality information for the USSR from which I have seen very few specimens. In this instance, literature records for political areas were accepted and are represented by unfilled boxes (□) which are placed over the former capital city of that political area. The majority of these records were obtained from Jakobson

(1905) and represent political divisions which no longer exist or are presently known by different names.

2.3.2.2 Interpretation of presumptive locality names

Within the Palearctic region, assignment of locality names to particular places is more difficult and complicated than in the Nearctic region. This is because of my lack of familiarity with Palearctic localities, lack of a country or regional name on many Palearctic specimens, differences in language and transliteration, as well as problems associated with interpretation of enigmatic or cryptic label data. Procedures used when confronted with these problems include: 1) Inference based on the collector (I have assumed that most collectors have collected within the vicinity of their geographic home or homeland). 2) Commonly used historical interpretations of locality names were generally accepted (*e.g.* "Königsberg" appeared commonly on locality labels. This was uniformly interpreted as "Kaliningrad, Russian S.F.S.R." 3) When a name refers to both a region and a populated place (*e.g.* Astrachan is both the name of a city and an oblast in Russian S.F.S.R., U.S.S.R.) I have consistently used the place name for purposes of mapping. 4) Transliteration is a particular problem with certain locality names (*e.g.*, the Siberian city, Čita, is rendered 'Tschita' in German, 'Chita' in English, *etc.*).

In this revision, I have followed the practice of recent international atlases, and used the official transliteration schemes adopted by the country in which localities are presently located (thus 'Čita', rather than 'Chita'; 'Astrachan' instead of 'Astrakhan').

5) Maximum concordance among all label data is important. For example, a label in Cyrillic script was transliterated as "Jakovskoje, Spas. u., Ussuri kr." and this was interpreted as "Jakovskoje, near Spassk Dal'niy in the former Ussuri Kraj of Russian S.F.S.R., U.S.S.R" even though modern atlases list many places with the name Jakovskoje, but none in the Ussuri region. Similarly, date of collection of specimens was used as an aid in choice of locality names. The presumptive locality must have been known by that name during a time span that includes the date of collection. For instance, the specimen referred to above was collected in 1926 and the Ussuri Kraj existed as an official entity only from 1926 until 1938 (Seltzer 1962). 6) Concordance of presumptive locality with known range of a species was used in examples where a choice between probable localities was necessary. If presented with a choice of presumptive localities, some of which were outside, and only one of which was inside the "known" range of a species, then the latter was accepted as "correct". The "known" range was decided on the basis of other, unambiguous locality information. 7) When the above methods failed, an appeal was made to colleagues or other workers who have specialized knowledge of various geographic areas. Finally, if all or some of these procedures were insufficient to determine

where a presumptive locality might be, then the locality name is listed under the heading "Locality not determined". In the list of specimens examined (available separately from me), my interpretation of problematic localities is given, for any locality "A", as "A [=A']" for locality interpretations which I think are probably correct, and as "A [?=A']" for less certain interpretations.

2.3.2.3 Sources of information about geographical localities

Many sources were used for tracing locality names. Most extensively used sources for place names were Bartholomew (1955, 1956, 1957, 1958, and 1959) and Seltzer (1962). The latter was particularly useful because of the historical treatment given various place or regional names. Most Nearctic localities were found by means of state and provincial maps. Many Canadian localities were found in the recent Energy, Mines and Resources, Canada (1980) atlas. Modern German and French language world atlases were essential. Other sources, used mainly for older names in the Palearctic region were Chisholm (1899) and Blackie (1887) which were especially useful for many 19th Century place names. Room (1979) was an invaluable source for following the changes of many place names from 1900 to 1978. Many European cities have been known by Latin names, and for interpetation of these, the works of Deschamps have served admirably.

2.3.2.4 An appeal for more complete labelling of specimens

Many specimens from European as well as North American collections do not include country names on the labels. This is most unfortunate because of time and effort required to obtain locality information. Two examples should suffice to demonstrate amount of time and effort wasted by taxonomists because of this oversight of collectors (previously including me). In the course of this study, a specimen received was labelled "S. Georgia" with no further information supplied (*i.e.* collector, date, or country). This locality information could be variously interpreted as: 1) southern Georgia, U.S.S.R., 2) southern Georgia, U.S.A., 3) south of Georgia, Vermont, U.S.A., 4) Strait of Georgia, British Columbia, Canada, or 5) South Georgia, an island in the South Atlantic Ocean. Application of procedure 6 noted above meant that the U.S.S.R. locality was most likely the correct one.

The second example concerns various abbreviations used for States or Provinces. For instance, the current abbreviation used by the U.S. Post Office for the Province of Alberta is "AB" while the abbreviation most commonly used by Canadians is "Alta". Unfortunately these abbreviations have been and are being used by collectors.

A colleague tells an informative anecdote concerning a recent trip to Europe during which he talked to a European lepidopterist who had traded specimens with workers in Alberta. This colleague was asked about the incredible diversity of butterflies occurring at "Alta, Colorado". Apparently the collector had made a choice between the four "Alta" localities which he could find in North America: Alta, Colorado; Alta, California; Alta, Iowa; and Alta, Utah, all of which are of course in the wrong country.

Problems associated with interpretation of label data and locality information probably account for a good deal of reluctance of some entomologists to study the fauna of other regions. This situation runs counter to the developing trend in insect systematics to consider the total fauna of groups so that more information is available for phylogenetic and zoogeographic analysis. It seems to me that much is lost and confusion and conflicts occur when a situation develops whereby there is a common fauna (in this example, Holarctic) but a vicariance of systematic workers. Part of the problem can be so easily solved by proper labelling of specimens.

2.4 Criteria for ranking taxa

2.4.1 Criteria for subgeneric rank

Subgenera are taxonomically useful and provide increased information within large, divergent genera or within smaller genera which encompass a subjectively large amount of divergence (see Ball and Roughley 1982). The latter is particularly true if the subgenera occupy different adaptive zones. Each subgenus must, however, represent a natural evolutionary unit, *i.e.* it must be monophyletic.

Taking these guidelines into consideration, I have recognized no subgenera within *Dytiscus*. Existing subgenera are nomenclaturally invalid and/or do not represent phylogenetically distinct clades. As well, I can discern no new adaptive zones of member taxa, nor does any group of species diverge sufficiently from the basic structural pattern enough to warrant subgeneric assignment.

2.4.2 Criteria for species-group taxa

Use of species-groups provides increased information and convienience without the demands and increased complexity of formal nomenclature. They represent an abbreviated notation for a group of species which are defined in a more complex manner. For instance, the group of species of *Dytiscus* which possess acuminate metacoxal processes are referred to herein as the *D. dauricus*-group. See Lindroth (1969:xxiii-xxiv) for further discussion of use of species-groups.

I have used species-groups for small monophyletic clades because of communicative value and ease with which these smaller groups are discussed in treatments of taxonomy, phylogeny, and zoogeography. I have not used any uniform manner in selecting the nominate taxon of species-groups. Instead, I have used the name of that taxon which represents a mental image of the species-group to me. The species-groups which I recognize are based on my reconstructed phylogeny (Fig. 30). These are:

D. verticalis-group:	*D. verticalis* Say
D. hybridus-group:	*D. harrisii* Kirby
	D. hybridus Aubé
	D. marginicollis LeConte
	D. habilis Say
D. semisulcatus-group:	*D. semisulcatus* Müller
	D. sharpi Wehncke
	D. carolinus Aubé
	D. fasciventris Say
	D. hatchi Wallis
D. dimidiatus-group:	*D. cordieri* Aubé
	D. dimidiatus Bergsträsser
	D. mutinensis Pederzani
	D. pisanus C. de Castelnau
D. marginalis-group:	*D. marginalis* Linnaeus
	D. persicus Wehncke
	D. delictus) (Zaitsev)
D. dauricus-group:	*D. latissimus* Linnaeus
	D. circumcinctus Ahrens
	D. alaskanus J. Balfour-Browne
	D. dauricus Gebler
	D. lapponicus Gyllenhal
	D. circumflexus Fabricius
	D. thianshanicus Gschwendtner
	D. latro Sharp
	D. sinensis Feng

2.4.3 Criteria for species level rank

Most animal taxonomists subscribe, at least nominally, to some form of Mayr's (1942) "biological" species definition. This, however, represents a theoretical ideal of how animals should behave, and is most difficult to test or even infer consistently or uniformly from the patchy samples characteristic of most analyses of taxa. After comparing and contrasting various species concepts used by botanists and zoologists and their uses and values in practice, Cronquist (1978:3) suggested that: "Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." Cronquist further details problems with strict use of a narrow or even a single species definition. Similarly, Hammond (1981a and b) has suggested that concepts of species and speciation built from experience with large, mobile vertebrates with low reproductive rates do not apply well to many insect groups.

The more important goals of the brief discussion above are to point out the need for a re-evaluation of species concepts by practicing animal taxonomists. Of paramount importance is the need for every taxonomist to state clearly the criteria for species recognition which they have used.

My study of taxonomic status of population samples of species of *Dytiscus* was hampered by low numbers of most samples, and samples from widely separated areas. Such disparate samples probably come about because of lack of collecting attempts in certain areas, difficulty of collecting large fast-swimming beetles, seasonal occurrence of adults, relatively low levels of abundance, and mensural bias of certain collecting techniques (see Measurements). While it is true that most species of *Dytiscus* so far encountered in the field are common to very abundant in the correct habitat at the correct time of year, it is also true that they are always at a relatively low density (*e.g.* see James (1970) for *D. fasciventris* and discussion of natural history in my treatment of *D. cordieri*). Low density is almost certainly a result of their status as major predators within most pond ecosystems.

I required a practical and useful means of delimiting species which could circumvent such problems. The most useful criteria I have found for delimitation of species of *Dytiscus* is form of apex of median lobe and sympatry. Characteristics of the median lobe are distinctive, so that even closely related species are consisently differentiated, and median lobes of male specimens of the same species from widely separated parts of the species range are similar. For instance, the median lobes illustrated in Figs. 18d and 19a are close to the extremes of variation found within a single putative species (in this example *D. circumcinctus*), yet the respective specimens are from Edmonton, Alberta, Canada and Berlin, Germany. Females were associated on the basis of co-occurrence with males and by general similarity in body shape and colour pattern. Sympatry of divergent forms was used as a corroborative test of species status. However, in examples for which no sympatry is known (*e.g. D. habilis-D. marginicollis, D. semisulcatus-D. sharpi*) difference in form of median lobe is considered sufficient for assignment to species status.

2.4.4 Criteria for recognition of subspecies

Mayr (1963, 1969) and Simpson (1961) provide thorough analyses of theoretical and genetic aspects of subspecies and subspeciation. Kavanaugh (1979:92-94) and Lafontaine (1982:9-10) presented balanced and valuable discussions of use of subspecific rank, and more importantly have expressed their practical criteria for recognition of subspecific status. I have accepted, amalgamated, and used the criteria of the latter two authors. Subspecific names are used for sets of population samples which are: 1) independent or isolated evolutionary units; 2) presently differentiated from other conspecific units but excluding differences thought to be ecophenotypic; 3) sufficiently phenotypically distinct that, except for similarity of aedoeagus of male specimens, they approach the amount of phenotypic divergence found among any two closely related species; and 4) of significance in analysis of historical zoogeography. Such populations are inferred to be isolated at present only by geographical gaps in range. If this barrier to gene flow is maintained for a sufficient period of time, then it is predicted that these populations will diverge sufficiently to preclude future mixing of genetic information. In short, subspecies status is used for inferred incipient species status.

The amount of meristic variation observed in most species of *Dytiscus* is quite low. I believe this is due in large part to various aspects of life history of these species, such as dispersal, which lead to a relatively large amount of panmixis. This explanation is further developed in the analysis of ecological relationships presented elsewhere. It is because of the normally uniform nature of most species that phenotypically distinct populations are quite apparent, *i.e.* they stand out. Therefore, my procedure for assignment of subspecific rank is recognition of allopatric populations of consistently distinct phenotype, but of which male specimens have sufficiently similar forms of the apex of the median lobe of the aedoeagus to be included in the same species.

2.4.5 Infraspecific categories other than subspecies

Literature concerned with taxonomy of European species of *Dytiscus* is replete with names for such infraspecific categories as variety, form and aberration. As such, and provided that they are truly intended as something other than subspecific levels, they are outside the jurisdiction of the *International Code of Zoological Nomenclature* and presumably each taxonomist is free to deal with them as seems appropriate. Within species of *Dytiscus* these names are predominantly used to express differences in sulcation of the elytra of female specimens. For instance, female specimens of *D. marginalis marginalis* vary in degree of elytral sulcation, from those with distinct elytral sulci to those with no trace of sulci, with every conceivable intermediate. However, the latter category is decidedly less numerically common in collections. These respective forms are generally named *forma typica*, ♀ var. *conformis* Kunze (even though Kunze described *conformis* as a distinct species), and ♀ var. *semicostatus* Reineck.

I believe that use of such names, some of which have no obvious descriptive value, to be retrogressive and needless. If Nearctic and other Palearctic species were all treated in a similar manner, then proliferation of names would be tremendous, but our understanding of this intriguing phenomenon would, I think, be diminished and obscured. In an attempt to increase the descriptive and therefore communicative value of variation in degree of elytral sulcation I have not recognized any names below the rank of subspecies and instead I have discussed it as occurring in two states: sulcate and non-sulcate. The former state includes all specimens with any trace of sulcation visible on the elytron. Use of these two states allows clear and unambiguous expression of any geographical pattern in elytral sulcation without detailed knowledge of the taxonomic history of a species.

3. Taxonomy

3.1 Discussion of taxonomically important characters

3.1.1 Sexual dimorphism

Adults of *Dytiscus* exhibit a number of characters which are sexually dimorphic. Excluding male and female genitalia, the most obvious of these are the following: 1) male specimens are broader and longer on average. 2) pronota of male specimens are wider at the base and less narrowed anteriorly; 3) profemora of males are bowed along their length and are more robust and more deeply emarginate ventrally; 4) male specimens have two tufts of long setae at the base of each profemur compared to one tuft of female specimens; 5) male protibiae are more robust and widened basally; 6) three basal protarsomeres of male specimens are laterally expanded and form a large subcircular acetabulum, with tarsomere I bearing two very large and numerous small suckers and tarsomeres II and III each with only numerous smaller suckers; 7) male mesotibiae are slightly longer and very slightly more robust; 8) male specimens with three basal mesotarsomeres elongated and widened to form an acetabulum, these tarsomeres bearing numerous small suckers; 9) some adult females of some species have 10 longitudinal narrow grooves or sulci on each elytron; 10) male specimens possess natatory setae on both the anterior and posterior faces of both the metatibiae and basal metatarsomeres, while female specimens bear natatory setae on the anterior faces of the metatibiae and on the posterior faces of basal metatarsomeres only.

3.1.2 Body size and shape

Despite the limitations of measurements of body length (see Measurements), I have made limited use of total length (TL) in distinguishing between members of certain pairs of species. Usually this is done where there is no overlap between the adults in size. However, TL is used also in examples where the majority of specimens of a species tend to be larger or smaller than the majority of specimens of another species treated in the other rubric of a couplet in the key. Ranges of lengths of specimens examined are shown in Table 2 for each species of *Dytiscus*. In general, the most common length of specimens is toward the upper end of the range, but there are a number of exceptions (*e.g.* compare information in Tables 1 and 2 for Nearctic specimens of *D. dauricus*).

Body shape (TL/GW) is relatively uniform among species of *Dytiscus* (Table 2, except *D. latissimus*). Differences in body shape are used in certain species pairs where there is no overlap of range in this ratio.

3.1.3 Head

Five taxonomic characters of the head are used. The anterior margin of the clypeus of specimens of most species is linearly transverse or slightly concave, whereas in specimens of *D. harrisii* and *D. latissimus* it is distinctly bisinuate. The posterior margin of the clypeus is normally on the same plane as the frons. In female specimens of *D. dauricus*, however, it is distinctly and abruptly raised above the level of the anterior margin of the frons, and is quite useful for diagnosing female specimens of this species.

All members of *Dytiscus* have a more or less distinct chevron-shaped pale mark on the frons between the eyes. Typically the lateral arms of the chevron are not expanded antero-laterally to reach the antennal bases, but in most specimens of some species where this does occcur, this character state is taxonomically useful. In some specimens, yellow coloration associated with increased chevron size extends posteriorly from the antennal bases along the inner margins of the eyes and thus forms an inverted M-like mark on the frons. However, members of only one species, *D. circumcinctus*, were observed to have the entire eye ringed with yellow on the dorsal surface.

3.1.4 Pronotum

Members of all species of *Dytiscus* have lateral yellow bands on the pronotum. Anterior and posterior bands are or are not present. Specimens of any given species vary in colour and, generally, lighter specimens of a taxon which would normally show no trace of, for instance, an anterior pronotal band, have a very narrow yellowish or reddish band. Characterization of relative width of anterior or posterior bands is quite important. For instance, in couplet 3 to Nearctic species, the alternatives are anterior band less than 0.4 versus more than 0.5 width of lateral band. I have not recorded a specimen of either category which is very close to these measurements. For instance, most specimens following the first alternative are in the range of 0.3 or less and those following the second alternative are in the range of 0.6 or more. Therefore, the values used in the key were chosen to allow for more variation than recorded and to avoid a strictly comparative character such as anterior pronotal band wider versus narrower. Even if exceptional specimens are encountered, subsequent comparison to the diagnostic combination of each species should allow discovery of misidentification.

The pronotum of most specimens of *Dytiscus* has a longitudinal, shallow channel near the lateral margin. When this character state is present the pronotum is described as explanate. Reduction or lack of an explanate pronotum is characteristic of the members of the *D. hybridus*-group and of male (but not female) specimens of *D. cordieri*.

3.1.5 Legs

Length of the apical pro- or mesotarsal segment is commonly used in the keys as an aid for determination, but in the form of a comparative rather than as an absolute numerical value. Pro- and/or mesotarsal claws are longer or shorter than pro- or mesotarsomere V, or the values are converted to a proportional value. Proportional length of protarsomere V to width of protibia, measured at the widest point, allows establishment of two species-specific categories for males of some species. Relative number of punctures on the anterior surface of protarsomere V is also used.

Male specimens of *D. hybridus* and *D. marginicollis* are distinctive in that mesotarsomeres II and III lack suckers from a small longitudinal area. Male specimens of all other species of *Dytiscus* have suckers evenly distributed over mesotarsal acetabula.

Coloration of metacoxal plates follows that of pterothoracic sterna discussed below.

Form of the metacoxal process varies considerably among sets of species but relatively little within species and therefore is of great taxonomic value for establishing major sections in the key. The inner margin of a metacoxal process is convex (*e.g.* Fig. 21a), or concave (*e.g.* Fig. 22k). Apically the metacoxal process is more or less rounded (*e.g.*

Fig. 21a), or the lateral margins form an acute angle (*e.g.* Fig. 22a), or the apex is drawn out into an elongate acuminate process of varied length (*e.g.* Fig. 22k).

Shape of the apex of the metatrochanter varies extensively within some taxa, is sexually dimorphic in some, and is characteristic in still others. When used as a taxonomic character, it occurs in two states: apex broadly rounded, or drawn out into a fine point apically (acuminate).

3.1.6 Elytra

Colour of elytra of most specimens is piceous to black with lateral yellow stripes. Many specimens have the lateral stripe abruptly curved inward pre-apically to form a more or less obscure subapical fascia, but in specimens of *D. verticalis* this fascia is quite distinctive because it is uninterrupted, broad, and highly contrasted with elytral ground colour. Elytra of specimens of *D. lapponicus* have a yellow ground colour with infuscation reduced to linear rows of small dots.

The elytral epipleuron is exceptionally expanded laterally in specimens of *D. latissimus* and accounts for much of the unique width and body shape characteristic of this species (Table 2). Specimens of *D. harrisii* have the epipleuron slightly widened but not nearly as greatly as in the former species. No other species shows expansion of the elytral epipleuron.

Elytra of some female specimens are sulcate. Sulci are narrow longitudinal depressions of the surface cuticle and each sulcus is separated from its neighbour by an inter-sulcal ridge. No female specimens of the Nearctic *D. verticalis*- or *D. hybridus*-groups that I have seen were sulcate. Among other species groups the proportion of sulcate and non-sulcate females veries greatly. Only in *D. carolinus* and *D. latissimus* were all female specimens observed sulcate. No sulcate females were seen of some Palearctic species (*e.g. D. delictus*), but this is probably due to the low numbers of specimens available for study. Relative length of eytral sulci is not used as a taxonomic character, but there is a phylogenetic trend toward increasing sulcal length. Members of certain taxa with very long sulci do have distinctive patterns. For instance, sulcate female specimens of *D. dauricus* have inter-sulcal ridges VII and IX (numbered from suture) curved toward each other and in contact, thus V-shaped, apically. The shorter intermediate ridges VIII and IX do not meet apically. Sulcate females of *D. alaskanus* have the respective members of each pair of ridges curving toward and apically in contact such that each pair forms its own exaggerated V-shape.

3.1.7 Pterothoracic and abdominal sterna

Colour pattern of abdominal and pterothoracic sterna is diagnostic given an understanding of infraspecific variation, which is relatively low among species of *Dytiscus*. Extremes in pattern are shown in Figs. 7 to 13. The median lobe of male specimens at the end points of colour variation were carefully examined to determine that they did indeed belong to a given taxon. In these figures, infuscation is shown as black, yellow as white, and red as various densities of stippling. The darker the red coloration, the more dense the stippling. These figures are mostly composite, *i.e.* they represent the lightest or darkest sterna respectively of series of species studied intensively. As such they should represent close to the extremes of specimens which will be encountered. This is somewhat dependent on the total number of specimens that I have examined. For instance, I have greater confidence that the limits of variation are approached in the representation of *D. marginicollis* (972 specimens examined), than in that of *D. persicus* (16 specimens examined). Important character states are presence or absence of red coloration, whether or not the abdominal and pterothoracic sterna are unicolorous piceous or black or yellow versus yellow with infuscated areas and if the latter than the relative amounts and positions of the infuscations.

3.1.8 Median lobe of aedoeagus

Exceptionally diagnostic and uniform characteristics are found in the shape of the apex of the male median lobe (Figs. 14-20). Of specimens examined, there is insignificant variation within species. I have not used length of the median lobe as a taxonomic character because this is probably correlated with variation in the total body length of specimens (see Measurements). Important character states of median lobe shape are: 1) comparative deflection of apex from line formed by basal portion of median lobe; 2) rounded versus irregular apex; 3) presence or absence of apical knob; 4) presence or absence of subapical, lateral notches; 5)width of apical knob relative to preapical width of shaft; and 6) overall similarity to that shown in the scanning electron micrographs.

3.1.9 Distribution

Perhaps the most desirable and easiest couplets to use are those which separate eastern and western species (*e.g. D. sharpi* and *D. semisulcatus*). The degree of confidence in the use of such couplets is related to amount of gap between ranges and degree to which the range of a species is known or at least the degree to which it can be predicted. When this confidence is fairly high, I have not hesitated to use range as a character of equal value to structural features. In the keys the geographic range of a species or subspecies is not used as the only character state because of numerous specimens with no or only cryptic label information.

3.2 Genus Dytiscus Linnaeus

Dytiscus Linnaeus 1758:411. Generitype – *Dytiscus marginalis* Linnaeus 1758:411, designated by Latreille 1810:426, attributing the species to Fabricius 1775:230. Curtis (1826:99), Westwood (1838:9), Crotch (1873:406), Guignot (1946:118), Leech (1948:413), Balfour-Browne (1960:252), and Guignot (1961:856) cite *D. marginalis* as generitype.

Hope (1839:131, 137), Duponchel (1845:154), Jacquelin du Val and Migneaux (1857:77), and Thomson (1859:12) designate *Dytiscus latissimus* Linnaeus 1758:411 as generitype.

Dyticus Müller 1776:69. **Incorrect emendation.**

Macrodytes Thomson 1859:12, 1860:41. Type species – *Dytiscus marginalis* Linnaeus 1758:411, by original designation. Subsequently designated as type species of subgenus *Macrodytes* by Guignot (1961:857, "...désigné ici."). Generitype – *Dytiscus conformis* Kunze 1811:58 (a junior synonym of *D. marginalis* Linnaeus), designated by Hope (1839:131), attributing the species to Stephens 1828:87.

Subgenus *Leionotus* Kirby 1837:76. Generitype – *Dytiscus franklinii* Kirby 1837:77 (junior synonynm of *Dytiscus dauricus* Gebler), by original designation.

Subgenus *Dyticopsis* Houlbert 1934:134. Generitype – *Dytiscus lapponicus* Gyllenhal 1808:468, here designated.

Description (Adults). - Size large, TL 22.0 to 44.0 mm, body form ovate (TL/GW 1.76 to 2.10 except *D. latissimus* 1.55 to 1.62), outline continuous, widest just behind middle. Colour dark brown to piceous, often with greenish cast, with yellow or reddish markings.

Surfaces shining, with singular isodiametric sculpture, microlines very fine and difficult to see except at very high magnifications; surface of some specimens dulled by dense accumulation of coarse pores at apex and/or base of elytra, laterally on pronotum, or on sulci of sulcate females.

Head. Large, prognathous, inserted firmly into thorax, without raised carinae. Labrum excised on anterior margin (except nearly truncate in *D. latissimus*), yellow to red, with brush of fine short hairs in emargination. Labro-clypeal suture distinct, evenly curved (bisinuate in *D. harrisii*). Clypeus distinct, yellow to red, clypeo-frontal suture present. Frons of most specimens dark brown to piceous or black, most specimens with yellow to red chevron and yellow to red markings over antennal bases and, on many specimens, on inner margins of eyes. Chevron of few specimens extending to antennal bases. Vertex short, dark brown to piceous or black. Occiput normally inserted into thorax. Eyes large, anterior margin not emarginate. Palpi and antennae yellowish to reddish-brown, articles of many specimens infuscated apically. Antennomeres elongated, glabrous, outherwise unmodified. Mandible with retinacular and two terebral teeth, and with with row of stiff, short setae ventrally. Maxilla with palpomeres elongated, glabrous, otherwise unmodified. Lacinia with apex acute and abruptly bent, setose on inner margin only. Galea with apex bluntly pointed and abruptly bent. Labium with palpomeres elongated, glabrous, otherwise unmodified. Mentum distinct, deeply emarginate at middle, with two low lobes in emargination, without setae. Submentum slightly wider than mentum, without setae. Gula narrowest just posterior to contact with submentum, wider apically, at narrowest 0.25 to 0.33 width of prementum, without setae. Further structural information about head in Sharp (1882:203-215), Buhlmann (1923:17-33), and Guignot (1933:13-19).

Thorax. Pronotum transverse, without carinae, with lateral margins acute but not margined, wider at base than at head, with lateral outline rounded, antero-lateral margins produced anteriorly as rounded lobes on either side of head. Dorsally glabrous, with base continuous with and overlapping bases of elytra, posterior margin more or less bisinuate on each side, majority of specimens explanate with linear depression laterally extended from anterior lobes to base, disc dark brown to black with lateral yellowish bands, some specimens with anterior and/or posterior yellowish to reddish bands. Ventrally with prosternum markedly compressed by enlarged procoxae, procoxae confluent-open-bridged (Bell 1967, Evans 1977, Baehr 1979). Prosternal process with ventral surface convex basally to flat apically, apex broadly rounded, marginal bead complete except apically. Further details of prothoracic structure in Sharp (1882:215-222), Evans (1977) and Baehr (1979). Mesosternum with mesocoxa of complex-type of Bell (1967), metepisternum contacting mesocoxal cavity (Dytisci complicati of Sharp 1882:964), further details of structure of mesosternum in Sharp (1882;222-228) and Evans (1977). Metasternum with short broad notch for reception of prosternal process, metasternal wing with antero-lateral margin not straight, metasternum wide, most specimens with shortest distance from mesocoxa to metasternum greater than width of metacoxa measured along same line, not reaching epipleuron. Metacoxae of incomplete-type of Bell (1965), metacoxal plates transverse, length approximately 0.5 width. Metafurca (metendosternite) with space between anterior rami narrow and short, base wide and transverse, with arm at each end (Crowson 1938 and 1944, F. Balfour-Browne 1944, Riha 1955:391-393).

Proventriculus. Bowl- or calyx-shaped, outer (main) lobes triangular, ciliate, and without teeth, inner (intermediate) lobes trianular (F. Balfour-Browne 1934, 1944).

Legs. Short, broad, sexually dimorphic in setation. Anterior and middle legs quite short, with strong sexual dimorphism of form, in repose retracted into prosternal-mesosternal cavity. Relative length (longest to shortest): femur, tarsi, tibia. Hind legs longer, without sexual dimorphism of form, highly modified for aquatic life, relative length: tarsi, femur, tibia. Further details of structure of legs in Sharp (1882:234-239, 246-257), Buhlmann (1923:48-64), Guignot (1933:34-44), and F. Balfour-Browne 1950:259-263).

Elytra. Continuous with outer margin of pronotum at base, widest just behind middle, apices rounded. Dorsal surface shining or dulled by dense, coarse punctation basally, apically and/or laterally, long fine setae on postero-lateral margin. Dark brown to black, many specimens with greenish cast, with lateral yellow margins, some specimens with sublateral transverse fascia. Lower surface without sublateral carina and ligula; subapical binding-patch of modified setae present (Hammond 1979).

Males with upper surface without sulci, female with or without sulci. Sulci sub-basal,in form of narrow shallow longitudinal trenches, ended from 0.5 to about 0.85 of elytral length. Further details of structure of elytron in Sharp (1882:241-243), Buhlman (1923:68-70), Guignot (1933:28-31) and Hammond (1979).

Metathoracic wings. Well-developed, no specimens observed to be brachypterous. Wedge cell present and well developed. Oblongum cell in shape of parallelogram, with M_4 vein attached anterior to middle. Distinct area of modified dense setae along posterior margin of cubitus vein near wing margin. Further details of structure of flight wing in Sharp (1882:243-246), Forbes (1922, 1926), Buhlmann (1923:64-67), Guignot (1933:32-33), Goodliffe (1939), F. Balfour-Browne (1944), Hammond (1979) and Ward (1979).

Abdomen. Dorsally with basal pleuron transversely grooved. Apical two pleura with stigmata markedly enlarged and transversely elliptical, these pleura densely covered with long setae. Sterna glabrous except some specimens with long fine scattered setae on last visible sternum. Various in colour, unicolorous black or yellow or marked with black, yellow, or red. Proportional length of visible sterna (longer to shorter): last, second, third, fourth, fifth and first subequal at epipleuron. Further details of structure of abdomen in Sharp (1882:239-241), Buhlmann (1923:72-77) and Guignot (1933:44-49).

Aedoeagus. Similar to that of *Hydaticus* (Roughley and Pengelly 1982:256-257, 295, figs. 4 and 5), except as follows: 8th sternum with deep narrow emargination, 9th pleuron with small longtudinal sclerite present on membrane, median lobe without lateral flanges, paramere without flange and with setae on antero-dorsal margin, preputial covering not complete to apex, incised, and epipenite absent. Further details of structure of aedoeagus are in Demandt (1924:209-275), Guignot (1933:49-58) and F. Balfour-Browne (1950:255-256).

Ovipositor. Apical sternum with deep narrow emargination extended to base, central portions membranous. Paraproct triangular with posterior margin membranous centrally. Valvifer articulated with stylomere I apically, of two lateral elongate struts joined by membrane. Vulval sclerite lamellate, without setae, inserted into stylomere I ventrally. Stylomere I elongate, sclerotized, acute apically, without setae and cultriform in shape. Further details of structure of ovipositor in Demandt (1924:151-209), Guignot (1933:58-67) and Burmeister (1976).

3.3 Key to adults of Nearctic Species of Dytiscus Linnaeus

1 (0) Metacoxal process with inner margin convex, apex rounded to obtusely angulate, but not acuminate (Fig. 21A-E, H-K) 2

1' Metacoxal process with inner margin concave, apex acutely angulate, more or less acuminate (Fig. 22F-H) 12

2 (1) Clypeus with anterior margin shallowly but distinctly bisinuate (Fig. 23A); pterothoracic sterna predominantly piceous to black, metacoxa and abdominal sternum I marked with yellow, sterna II to V or II to VI with reddish markings (Fig. 7B) .. .. *D. harrisii* Kirby

2' Clypeus with anterior margin straight or slightly concave (Fig. 23B); ventral markings various 3

3 (2') Pronotum with anterior yellow band absent, or, if present, less than 0.4 width of lateral bands Figs. 1A, D, 2C-E) 4

3' Pronotum with anterior yellow band of most specimens more than 0.5 width of lateral bands (Fig. 1B, C) 9

4 (3) Pterothoracic and abdominal sterna piceous to black....................................5

4' Pterothoracic and/or abdominal sterna with yellow or reddish markings 7

5 (4) Pronotum with lateral margins not explanate; males with mesotarsomeres II and III with median glabrous area ventrally; females not sulcate.
.... *D. hybridus* Aubé

5' Pronotum with lateral margins explanate; males with mesotarsomeres II and III with uniform distribution of ventral suckers; females sulcate or not 6

6 (5') Size larger, TL from 29.6 to 36.0 mm; elytron with yellow subapical transverse fascia (Fig. 1A); females not sulcate .... *D. verticalis* Say

6' Size smaller, TL from 22.0 to 26.1 mm; elytron without yellow subapical transverse fascia (Fig. 2C); females sulcate.
.... *D. carolinus* Aubé (in part)

7 (4') Metepisternum, metasternal wings and metacoxae predominantly piceous to black, abdominal sterna black with reddish to piceous markings (Fig. 8D); distribution more southern, Atlantic Coast (Connecticut, south to Georgia), Gulf Coast, and northward along Mississippi River valley (Fig. 25C).
.... *D. carolinus* Aubé (in part)

7' Metepisternum, and metacoxae predominantly testaceous, abdominal sterna testaceous with black markings (Fig. 9A, B); distribution more northern and western 8

8 (7') Males with protarsal claws of most specimens longer than protarsomere V (Fig. 23C); females with mesotarsal claws longer than mesotarsomere V (Fig. 23E); pronotum more broadly margined with yellow (Fig. 2E); distribution west of Rocky Mountains from central California to northern British Columbia .... *D. hatchi* Wallis

8' Males with protarsal claws of most specimens shorter than protarsomere V (Fig. 23D); females with mesotarsal claws shorter than mesotarsomere V (Fig. 23F); pronotum more narrowly margined with yellow (Fig. 2D); transcontinental in northern North America .... *D. fasciventris* Say

9 (3') Pronotum distinctly explanate; protarsal claws subequal to protarsomere V; abdominal sterna yellow with baso-lateral infuscations (Fig. 9A, B) 8

9' Pronotum not or indistinctly explanate; protarsal claws much shorter than protarsomere V; abdominal sterna predominantly yellow (Fig. 9C) or predominantly black with various coloured markings (Fig. 7D, 8A) 10

10 (9') Pterothoracic and abdominal sterna testaceous to pale rufous (Fig. 9C); frons of most specimens with chevron extended to antennal bases (Fig. 23B); females with pronotum shallowly explanate, some specimens with elytron sulcate.... *D. cordieri* Aubé

10' Pterothoracic and abdominal sterna with extensive infuscation (Figs. 7D, 8A); frons with chevron not extended to antennal bases (*e.g.* Fig. 23A); females with pronotum not explanate, elytron not sulcate 11

11 (10') Pronotum with discal infuscation narrower than lateral yellow band (Fig. 1C); male with mesotarsomeres II and III with uniform distribution of suckers ventrally; distribution as in Fig. 24D. .... *D. habilis* Say

11' Pronotum with discal infuscation wider than lateral yellow band; male with mesotarsomeres II and III with median glabrous area ventrally; distribution as in Fig. 24D .... *D. marginicollis* LeConte

12 (1') Eye enclosed dorsally by narrow yellow band, or, some specimens with band narrowly broken near inner posterior margin of eye; pterothoracic and abdominal sterna testaceous to pale rufous, basal margins of sternum I very narrowly infuscate in some specimens (Fig. 11D).
.... *D. circumcinctus* Ahrens

12' Eye not enclosed dorsally by narrow yellow band, some specimens with inner margin margined with yellow or red; pterothoracic sterna with at least metasternum medially infuscate (Fig. 12A, B), abdominal sterna various in colour pattern 13

13 (12') Male with apical portion of median lobe sinuate laterally and apical knob distinct in dorsal view (Fig. 19C); females with postero-median margin of clypeus distinctly raised above level of frons along clypeal suture; sulcate females with ridges of sulci VII and X fused apically, and those of VIII and IX not fused apically; size larger, TL from 29.7 to 40.0 mm .... *D. dauricus* Gebler

13' Male with apical portion of median lobe evenly curved laterally and apical knob indistinct in dorsal view (Fig. 19B); females with postero-median margin of clypeus on same level as frons along clypeal suture; sulcate females with ridges of sulci VII and X, and of VIII and IX fused apically forming a 'V-V' pattern (Fig. 5A); size smaller, TL from 22.6 to 30.2 mm.
.... *D. alaskanus* J. Balfour-Browne

3.4 Key to Adults of Palearctic Species of Dytiscus Linnaeus

1 (0) Metacoxal process with inner margin convex, apex rounded to obtusely angulate, not acuminate (Figs. 21F, G, L-N) 2

1' Metacoxal process with inner margin concave, apex acutely angulate and more or less acuminate (Figs. 22E-N) 11

2 (1) Pronotum with anterior and posterior yellow bands absent (Figs. 21F, G, L-N), OR, less than 0.33 width of lateral band (Figs. 2A, B, 3B, C)........3

2' Pronotum with anterior and posterior yellow bands present and at least 0.50 width of lateral band (Fig. 3D) 6

3 (2) Pterothoracic sterna piceous to black (Figs. 8B, C); smaller specimens, 24 to 30 mm 4

3' Pterothoracic sterna predominantly yellow (Figs. 9D, 10A); larger specimens, 28 to 39 mm ...5

4 (3) Metatrochanter with apex rounded (Fig. 21F); body narrowly oval (TL/GW 1.97 to 2.01); distributed from Europe, east to Kazakh SSR, and New Zealand. .... *D. semisulcatus* Müller

4' Metatrochanter with apex acuminate (Fig. 21G); body broadly oval (TL/GW 1.84 to 1.94); distributed in Japan, Maritime USSR, northeastern China. .... *D. sharpi* Wehncke

5 (3') Body oblong (TL/GW 1,98 to 2.00); male with protarsomere V about 1.3 length of longer claw (Fig. 23G), and about 30 punctures on anterior surface; smaller specimens, 28 to 35 mm; distributed in Italy, Corfu, Yugoslavia.
.... *D. mutinensis* Pederzani

5' Body more elongate (TL/GW 1.84 to 1.95); male with protarsomere V about 1.5 length of longer claw (Fig. 23H), and about 60 punctures on anterior surface; larger specimens, 32 to 39 mm; distributed from Europe to Transcaucasia, Asia Minor and Syria
.........................*D. dimidiatus* Bergstrasser

6 (2') Metacoxal process with apex rounded (Figs. 21N, 22D) 7

6' Metacoxal process with apex acute (Figs. 22A-C) ..8

7 (6) Metatrochanter with apex acuminate (Fig. 21N); male with protarsomere V about 1.3 times width of protibia; male with median lobe broadly rounded at apex (Figs.17B); female with mesotarsomere V about 2.0 times length of IV (Fig. 23I); most females with elytron sulcate; distribution circum-Mediterranean.
.... *D. pisanus* LaPorte de Castelnau

7' Metatrochanter obtusely rounded; or acute (males, Fig. 22D); male with protarsomere V about equal in length to width of protibia; male with median lobe notched laterally at apex (Figs. 18B); female with mesotarsomere V about 1.5 times length of IV (Fig.23J); no sulcate females known; distributed in Maritime USSR .... *D. delictus* (Zaitzev)

8 (6') Venter with at least abdominal sterna II, III and VI with large, transverse, baso-lateral infuscation (Fig. 10D, 11A) 9

8' Venter with abdominal sterna II to V without baso-lateral infuscation, or, with only narrow baso-lateral infuscation (Fig. 10C) 10

9 (8) Head with chevron extended antero-laterally to yellow spot at antennal base; Maritime USSR and Japan .....*D. marginalis czerskii* Zaitsev (in part)

9' Head with chevron not extended antero-laterally, not connected to yellow spot at antennal base; Caucasus Mountains, Transcaucasia and Crimean USSR, northeastern Turkey and Iran. .... *D. persicus* Wehncke

10 (8') Head with chevron extended antero-laterally to yellow spot at antennal base; Maritime USSR and Japan .....*D. marginalis czerskii* Zaitsev (in part)

10' Head with chevron not extended antero-laterally, not connected to yellow spot at antennal base; distributed from Portugal and southern Spain north to Scotland and east to Siberia. .... *D. marginalis marginalis* Linnaeus

11 (1') Elytron with epipleuron greatly widened into a flange (Fig. 4B); clypeus of most specimens with anterior margin shallowly bisinuate; distributed from France through Ukrainian SSR to western Siberia .... *D. latissimus* Linnaeus

11' Elytron with epipleuron not widened into flange; clypeus with anterior margin evenly curved 12

12 (11') Pronotum very broadly margined with yellow, anterior or posterior bands wider than or almost as wide as discal infuscation (Fig. 5C); elytral disc of most specimens with infuscation reduced to numerous lines of spots (Fig. 5C); metacoxal processes with apical spine very long (Figs. 22I, J) .... (*D. lapponicus*) 13

12' Pronotum more narrowly margined with yellow, anterior and posterior bands much narrower than discal infuscation (Fig. 5D); elytral disc piceous to black (Fig. 5D); metacoxal processes of various lengths (Figs. 22K-N) 14

13 (12) Pronotum with quadrangular infuscation (Fig. 5C); head with chevron V-shaped; distributed in northern Europe and USSR (Fig. 28D).
.... *D. lapponicus lapponicus* Gyllenhal

13' Pronotum with infuscation greatly reduced, almost linear, in shape of printers bracket, opening posteriorly; distributed in Italian Alps (Fig. 28D).
..................*D. lapponicus disjunctus* Camerano

14 (12') Metacoxal process with apical spine very long (Fig. 22K-N) 16

14' Metacoxal process with apical spine shorter (Fig. 22F-H) 15

15 (14') Eye enclosed dorsally by narrow yellow band, or, some specimens with band narrowly broken near inner posterior margin of eye; pterothoracic and abdominal sterna testaceous to pale rufous, basal margins of sterna I to III very narrowly infuscate in some specimens (Fig. 11D); male with apex of median lobe not sinuate in dorsal view (Fig. 18D).
.... *D. circumcinctus* Ahrens

15' Eye not enclosed dorsally by narrow yellow band, some specimens with inner margin margined with yellow or red; pterothoracic sterna with at least metasternum medially infuscate (Fig. 12B), abdominal sterna variable in colour pattern; male with apex of median lobe sinuate in dorsal view (Fig. 19C) .... *D. dauricus* Gebler

16 (14) Abdominal sterna with broad fasciae (Fig. 13A left, D) 17

16' Abdominal sterna without, or with very narrow fasciae (Fig. 13A right, B, C) 18

17 (16) Distributed in Europe, Great Britain, southern Scandinavia and northern Africa (Fig. 29A); male with protarsal claw about 0.50 length of protarsomere V; male with knob of median lobe not spatulate in lateral view (Fig. 20A). .... *D. circumflexus* Fabricius (in part)

17' Distributed in Peoples Republic of China (Fig. 29D); male with protarsal claw about 0.67 length of protarsomere V; male with knob of median lobe spatulate in lateral view (Fig. 20D). .... *D. sinensis* Feng

18 (16) Distibuted in Western Palearctic (Fig. 29A). .... *D. circumflexus* Fabricius (in part)

18' Distributed in central and eastern Palearctic (Figs. 29B, C) 19

19 (18') Head with chevron extended to antero-lateral margin; male with median lobe in dorsal view with pre-apical portion narrow (Fig. 20C); distributed in far eastern USSR (Fig. 29C) ......*D. latro* Sharp

19' Head with chevron not extended to antero-lateral margin; male with median lobe in dorsal view with pre-apical portion broad (Fig. 20B); distributed in central USSR and Afghanistan (Fig. 29B) .... *D. thianshanicus* Gschwendtner

3.5 **Dytiscus verticalis** Say, 1823

Dytiscus verticalis Say, 1823:92 (Type area- United States. Type probably lost, see below.). —Zimmermann, 1920:255. —Hatch, 1928:226. —Wallis, 1950:51. —Wallis and Larson, 1973:110 —Larson, 1975: 396.

Derivation of specific epithet. – Unclear but probably derived from Latin, meaning at the vertex, directly overhead or upright, possibly referring to the chevron on the vertex of the head.

Notes about type material. – As with most of the typical material of Thomas Say, original specimens are probably lost (Lindroth and Freitag 1969). However Say's original description is sufficiently diagnostic to indicate that this is indeed the taxon to which he was referring. Therefore a neotype is not needed.

Diagnostic combination. – Large size, sub-apical transverse fascia of elytron, infuscate venter, and pronotum with broad yellow lateral margins, permit easy recognition of adults of this Nearctic species.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 1A; coloration of pterothoracic sterna and abdominal terga in Fig. 7A; median lobe of male in Fig. 14A; and metacoxal processes in Fig. 21A.

Variation. – Adults are relatively uniform in coloration. Pronota and elytra of a very few specimens have a dark greenish cast. The sub-apical transverse fascia of the elytron varies in width and distinctness and is absent from a few specimens. Pronota of a few specimens have the anterior and posterior margins marked with yellow bands, less than 10% of width of lateral bands. Some other specimens have piceous anterior and posterior margins of the pronotum.

Natural history. – Both adults and larvae of this species seem to be most common in ponds associated with the eastern deciduous forests and adjacent areas. Data on labels are interpreted as evidence for an autumnal emergence from the pupal stage (Table 4). Autumnal dispersal could take place soon after emergence from the pupa as a teneral specimen from Ann Arbor, Michigan, was taken at a porch light in July (Tables 4 and 5). Other data suggestive for an autumnal dispersal flight are listed in Table 5. No information is available about overwintering sites, *i.e.* in water or on land, but adults of *D. verticalis* appear to have a vernal dispersal (Table 5). This vernal dispersal could allow adults to feed in temporary pond habitats before going on to more permanent breeding sites. They have been taken in temporary ponds twice in Ontario, near Huntsville 31.v.72 and 7.vi.66 (2 ROMC).

Distribution. – Map, Fig. 24a. This is a species of eastern North America which ranges as far west as western Ontario and Wisconsin and as far south as North Carolina with one dubious record from Homestead, Florida (1 MCZC).

Records of this species from the State of California [Stan. U. 19.iv. – (2 CASC) and a state record only (1 ICCM)] are probably in error.

Chorological relationships. – *D. verticalis* is broadly sympatric with all other Nearctic species which occur in eastern North America except the more northerly *D. dauricus* and *D. alaskanus*.

Phylogenetic relationships. – The basal segment of the labial palpus of third instar larvae of *D. verticalis* lacks the false segmentation of every other known third stage larva of *Dytiscus* (Wilson 1923, Fig. 37 and Roughley, unpublished data) and in this state they are similar to third stage larvae of *Hyderodes shuckardi* Hope (Watts 1964, Fig. 16).

Due to the distribution of this character state, I have placed members of *D. verticalis* as the sister group to the remainder of *Dytiscus*.

Material examined. – A total of 695 adult specimens were examined of which 302 are males, 388 are females, and for 5 specimens sex was not determined.

3.6 **Dytiscus harrisii** Kirby, 1837

Dytiscus harrisii Kirby, 1837:76 (Type area– "taken in the Journey from New York to Cumberland-house." Holotype–see Larson 1975:397.). –Zimmermann, 1920: 242, 248. –Hatch, 1928:277. –Hatch, 1953:238. –Gordon and Post, 1965:25. –Wallis and Larson, 1973:110. –Larson, 1975:397.

Derivation of specific epithet. – Kirby named this species in honour of T.W. Harris, "...a very eminent American entomologist."

Diagnostic combination. – Bisinuate anterior margin of clypeus, large size, and combination of distinctive dorsal and ventral colour pattern (Figs. 1B and 7B) allow easy recognition of adults of this species.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters of adult males and females are given in Table 3. Dorsal view of the body is shown in Fig. 1B; coloration of pterothoracic sterna and abdominal terga in Fig. 7B; median lobe of male in Fig. 14B; and metacoxal processes in Fig. 21B.

Variation. – Adults are relatively uniform in coloration. Pronota and elytra of a very few specimens have a dark green cast. Colour of legs varies, with the posterior faces of the pro- and mesofemora testaceous in some specimens, rather than the usual piceous to black. This difference is not completely correlated with geographic locality of the specimen but is more common in eastern North

America. The subapical transverse fascia of the elytron varies in width and distinctness but is present in all specimens examined.

Larson (1975) commented on the small size of specimens from Alberta and Northwest Territories compared to specimens from Ontario and Wisconsin. A similar difference was found in the course of this study, and is interpreted as indicative of sampling bias (see Measurements). Differences in length can be explained by a greater size range for adult *D. harrisii* in northwestern North America with smaller specimens being more often captured, whereas, in eastern North America the size range is smaller and therefore the adult stage appears to be larger within this area.

Natural history. – I have evidence that larval development takes place in or near running water. The remainder of the life cycle can be inferred from information on labels of adult specimens examined. Adults probably overwinter in relatively permanent water bodies [Vermont, Burlington, 22.ii.49, taken through fishing hole in ice, L. Champlain, (1, UVCC)]. Depending on local climatic and other factors, larval development is completed by June or July as indicated by occurrence of teneral adult specimens (Table 4), and mature, field-collected pupae [Alberta, Kneehills Creek near Acme, pupa coll'd. 23.vi.80, adult emg'd. 6.vii.80, (1, UASM); British Columbia, 1 km N Golden, prepupa coll'd 21.vi.80, adult emg'd 10.vii.80 (1, UASM)]. The adult teneral specimen from southern Alberta, 3.ix.61, reported by Larson (1975:398) probably represents an exceptional situation. Following shortly after adult emergence is a dispersal flight (Table 5), presumably to overwintering sites but possibly to localities where feeding takes place before overwintering begins. During these dispersal flights specimens are collected in non-typical habitats such as beach drift, and swimming pools (Table 5).

Distribution. – Map, Fig. 24B. The range of this species is transcontinental in the Nearctic region, from Newfoundland to Alaska. The northern limit of distribution is probably coincident with treeline and the southern limit appears to be Rhode Island, Nebraska and Washington. Most specimens are from states and provinces in the vicinity of the Great Lakes.

Chorological relationships. – *D. harrisii* is sympatric with other Nearctic species of *Dytiscus* except *D. habilis* and *D. carolinus*

Phylogenetic relationships. – This species is probably related to a species complex which includes *D. habilis*, *D. hybridus*, and *D. marginicollis*.

Material examined. – A total of 548 adult specimens were examined of which 259 are males, 277 are females, and for 12 specimens sex was not determined.

3.7 **Dytiscus hybridus** Aubé, 1838

Dytiscus hybridus Aubé, 1838:116 (Type area—"Etats Unis d'Amérique." Type not seen.). —Zimmermann, 1920:248. —Hatch 1929:226. —Hatch 1933:11. —Wallis 1950:51. —Gordon and Post 1965:24. —Wallis and Larson 1973:110. —Larson 1975:398.

Leionotus compar Melsheimer, 1844:26 (Type area — "Pennsylvania and Massachusetts." Type not seen.). —Zimmermann 1920: 248.

Derivation of specific epithet. — From the Latin *hybrida* meaning a hybrid or an indication of hybridization, presumably because, to Aubé, adults of this species demonstrated a mixture of the characteristics of other species.

Notes about type material. — I searched for, but was unable to find, any type material within the R. Oberthür collection in MNHN.

Diagnostic combination. — Adults of *D. hybridus* are distinguished from adults of other species of *Dytiscus* with piceous to black venters, by smaller size, non-explanate pronotal margins, and presence of wide yellow margins laterally only on pronotum. Females not sulcate. Males with mesotarsomeres I to III ventrally with longitudinal glabrous area.

Description. — Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters of adult males and females are given in Table 3. Dorsal view of the body is shown in Fig. 1D;

coloration of pterothoracic and abdominal sterna in Fig. 7C; median lobe of male in Fig. 14C; metacoxal processes in Fig. 21C.

Variation. – The most conspicuous variation of adult *D. hybridus* is in coloration of the pronotal margin. The most common condition is absence of posterior pronotal yellow band but with a very narrow anterior band. Some specimens have both the anterior and posterior bands obliterated and still others have both of these bands present and distinct. In examples of the latter, the anterior band is wider than the posterior band, and both are less than 0.33 width of a lateral band.

Other than pronotal bands, adults of this species are quite uniform in colour and in structural features. Most other differences in colour (*e.g.* piceous rather than black venter) are probably due to age of specimens when collected (*e.g.* fully sclerotized versus teneral). Compared to most other species of *Dytiscus*, *D. hybridus* occupies a smaller geographic range and is structurally more homogeneous.

Natural History. – Apparently this is a species which prefers mature ponds within the eastern deciduous forests of North America.

Collection of an adult female in December at Ithaca, New York (Table 5) could be interpreted as evidence that the adult stage overwinters in water. However, specimens have been collected in flight in Pennsylvania in December and in Illinois in January, and may indicate dispersal from any over-wintering habitat. Teneral specimens from the more southerly portions of the range were taken in June and July (Table 4). Specimen data indicative of flight period is inconclusive (Table 5); adults may have only an extended late-season flight (July to January) depending on geographic location, or a late season flight (July to September) and a very early season flight (December to January).

Distribution (Map, Fig. 24C). – This strictly Nearctic species appears to be common only east of the 100th meridian. Scattered localities, perhaps indicating range expansion (Larson 1975:398), extend the range to Oregon and northward into Alberta. The southern limit is represented by specimens from Missouri, Tennessee, and North Carolina. The hiatus in locality information in the eastern USA which coincides with the eastern mountain chains could be indicative of less collecting effort, lack of suitable habitat within the area, or of avoidance of montane habitats by adults of this species. The most north-central and north-eastern "limits" are probably artificial and due to insufficient collecting.

Chorological relationships. – Within the *D. hybridus* species group, *D. hybridus* is broadly sympatric with *D. harrisii* only.

Phylogenetic relationships. – Adults of this species exhibit a high number of plesiotypic character states when compared to other members of the *D. hybridus* species group. As such, of the four extant taxa, it is probably the most similar to the hypothetical ancestor of this clade (see Phylogeny).

Material examined. – A total of 1618 adult specimens were examined, of which 843 are males, 769 females, and 6 of undetermined sex.

3.8 Dytiscus marginicollis LeConte, 1845

Dytiscus marginicollis LeConte 1845:201 (Type locality–"in flumine Missouri". Holotype female in LeConte collection of MCZC labelled as follows: [green circular label]; Type 6091 [red label]; D. marginicollis Lec., albionicus Motsch.). –Zimmermann 1920:252 (*ex parte*). –Hatch 1929:226, 1933:11. –Leech 1941:290, 1948:414. –La Rivers 1951:404. –Hatch 1953:238. –Leech and Chandler 1956:323. –Anderson 1962:73. –Larson 1975:398.

Dytiscus albionicus Motschulsky 1859:166 (Type locality–Fort Ross near San Francisco, California, U.S.A. Type not seen.). –Zimmermann 1920:244.

Dytiscus fusco-striatus Motschulsky 1859:167 (Type locality–"St. Francisco", California, U.S.A. Type not seen.). –Zimmermann 1920:248.

Dytiscus anxius, Gemminger and Harold 1868:461, *nec* Mannerheim 1843:461.

Dytiscus anxius var. *albionicus*, Gemminger and Harold 1868:461. –Zimmermann 1920:244; *nec* Mannerheim 1843:461, *nec* Motschulsky 1859:166.

Dytiscus vexatus, Hatch 1929:226, *nec* Sharp 1882:643.

Derivation of specific epithet – From Latin *marginare*, to enclose within a border, and *collum* meaning neck, in reference to the yellow margins of the pronotum.

Notes about type material. – My interpretation of the placement of the Motschulsky names cited above differs from that of Larson (1975:401), who assigned them to

D. circumcinctus. Reassignment is based on absence of *D. circumcinctus* from California, USA, from which Motschulsky described both *D. albionicus* and *D. fuscostriatus*. Also, *D. marginicollis* is the only taxon occurring at the type localities for which Motschulsky would have described the venter as "*infuscatus*" (*D. albionicus*) or "*testaceis*" (*D. fuscostriatus*). Examination of Motschulsky's types will be helpful in determining proper placement of these names.

Diagnostic combination -- Distinctive pronotal and ventral coloration (Fig. 7D) separate adults of this Nearctic species from those of all other species except *D. habilis*. Adult males of *D. marginicollis* distinguished from males of *D. habilis* by mid-ventral glabrous areas on mesotarsomeres II and III. Males and females of *D. marginicollis* also have an increased area of the pronotal disc infuscate and the posterior margin of this infuscation is sinuate. Adults of *D. marginicollis* are longer, than those of *D. habilis* (Table 2). Females of both taxa are not sulcate. The range of *D. habilis* is south of that of *D. marginicollis*.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is not shown; coloration of pterothoracic sterna and abdominal terga is shown in Fig. 7D; median lobe of male in Fig 14D; and metacoxal processes in Fig. 21D.

Variation. – One of the most consistent character states shown by adult specimens of *D. marginicollis* is sinuation of anterior and posterior margins of the discal infuscation of the pronotum. This state has permitted rapid and efficient sorting of members of this taxon. In contrast, there is extreme variation in colour of the scutellum and, to a lesser extent, of legs. The scutellum varies from completely yellow to completely piceous in most population samples. Leg colour varies similarly, and these two states are not completely correlated, although there are general trends to extremes of both states in some specimens. Some specimens have elytral disc with obsolete irrorations. Post-mortem changes can discolor ventral and dorsal colour patterns. These are usually easily overcome by proper cleaning of specimens. Other structural and colour characters are relatively uniform.

Natural history. – Most habitats where I have collected adults of this species are characterized by high salinity, typical of ponds in grassland areas, and stands of *Scirpus* species. Larson (1975:399) noted an affinity for what were presumed to be permanent prairie sloughs in conjunction with *Typha* and *Juncus*.

Flight records are available for many months of the year, with July predominating (Table 5). Dispersal could follow shortly after emergence from pupae, as records of teneral specimens range from May to August (Table 4).

Taxonomic notes – Leech (1948) noted that two male specimens which he examined from Baja California, Mexico, might represent a distinct subspecies as they are more parallel-sided than other specimens. I have seen these specimens and judge them to be within the range of variation shown by more northern specimens.

Distribution (map, Fig. 24D) – The range of this species is perhaps significantly, if broadly, described as west of that of *D. hybridus* and north of that of *D. habilis*. The eastern-most record is from Aweme, Manitoba, Canada, and the southern-most from San Dimas, Durango, México. Records of this taxon from Alaska (e.g. Hatch 1929, Leech 1948, Larson 1975) are suspect, and could stem from the inclusion of *D. marginicollis* as a junior synonym of *D. anxius*, the type locality of which is Sitka, or from Hatch's inclusion of *D. vexatus* as a junior synonym of *D. marginicollis*. However, further collecting could well extend the range of this species northward along the British Columbia coast and perhaps into Alaska. The northern-most records of adult specimens are from Calgary and Lethbridge, Alberta, Canada, although I have seen mature larvae from George Lake, near Dunstable, Alberta (Roughley, in prep.). The record for the state of Durango, México, mentioned above, may seem inconsistent except that I have many larval records from Baja California, Mexico (and none for *D. habilis*, Roughley, in prep.) and the Durango specimen may represent disperal from Baja California del Sur.

Chorological relationships – The exclusively western North American distribution of *D. marginicollis* excludes sympatry with *D. carolinus* and *D. verticalis*. It is only narrowly sympatric or parapatric with *D. hybridus* and *D. habilis*.

Phylogenetic relationships – Within the *D. hybridus* assemblage, adults of *D. marginicollis* are most similar in colour pattern to those of *D. habilis* and these two species are more similar to *D. harrisii* than to *D. hybridus*. Despite these similarities, *D. marginicollis* is probably the sister species to *D. hybridus* based on common possession of glabrous areas on the male mesotarsomeres (Table 3).

Material examined – A total of 972 adult specimens were examined, of which 443 are male, 526 female, and sex was not determined for 3 specimens.

3.9 **Dytiscus habilis Say, 1834**

Dytiscus habilis Say 1834:441 (Type area–"...in the river beyond Vera Cruz...", Mexico. Type probably lost.). –Zimmermann 1920:248. –Darlington 1938:84 –Wallis 1950:51.

Derivation of specific epithet – This name is derived from the latin *habilis*, meaning apt, fit, suitable (Brown, 1956).

Notes about type material. – Say's types are probably lost (see equivalent section under *D. verticalis*). Since Say's original description agrees well with the present concept of this taxon (specimens within the LeConte collection, MCZC, belong to this taxon), and considering that *D. habilis* is the only species which is widespread in México, a neotype is not required.

Diagnostic combination. – See discussion under equivalent section in treatment of *D. marginicollis*.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 1C; coloration of pterothoracic sterna and abdominal terga in Fig. 8A; median lobe of male in Fig. 15A; and metacoxal processes in Fig. 21E.

Variation. – Most of the types of variation discussed under *D. marginicollis* apply equally well to *D. habilis*.

Natural history. – Nothing has been published concerning natural history of this species. Available flight records are for April and October in Chihuahua, México, and

June in Arizona, USA (Table 5). Specimens have been taken at elevations up to 2010 m [Chihuahua, 5.1 km n Colonia Garcia, 23.vii.79 (1 UASM)]. Other label information is scarce but the specimen mentioned above was taken at the margin of a creek, and another Méxican specimen [Chiapas, San Cristóbal de las Casas, 6.vii.64 (1 CASC)] was taken in a habitat characterized as "pond and spring".

Distribution (map, Figure 24D). – From southwestern Arizona, southeastern New Mexico, and southwestern Texas, USA, this species ranges southward to Guatemala.

Chorological relationships. – Along the northern edge of its range, *D. habilis* is either narrowly sympatric or allopatric with *D. marginicollis*. It is not sympatric with, nor does its range closely approach, that of any other species of *Dytiscus*.

Phylogenetic relationships. – The similarity to specimens of *D. marginicollis* was noted in discussion of that species. *D. habilis* is interpreted as representative of the lineage sister to that of *D. hybridus* plus *D. marginicollis*.

Material examined – A total of 240 adult specimens were examined, of which 148 are males, 90 females, and 2 of undetermined sex.

3.10 **Dytiscus semisulcatus** Müller, 1776

Dytiscus semisulcatus Müller 1776:70 (Type area—Denmark. Type not seen.). —Zimmermann 1920:253. —Guignot 1933:709. —Houlbert 1934:132. —Zimmermann and Gschwendtner 1938:38. —Guignot 1947a:242. —F. Balfour-Browne 1950:268. —F. Balfour-Browne 1953:27. —Zaitsev 1953:324. —Guignot 1961:857. —Ordish 1966:254. —Ordish 1967:6. —Galewski 1971a:100. —Schaeflein 1971:87. —Franciscolo 1979:662.

Dytiscus punctulatus Fabricius 1777:238 (Type area - "Chilonii in rivulus". Type not seen.). —Zimmermann 1920:253.

Dytiscus frischi Bergsträsser 1778:43 (Type locality—Hanau area of Hessen, West Germany. Type not seen.). —Zimmermann 1920:254.

Dytiscus stagnalis Fourcroy 1785:66 (Type locality—Paris, France. Type not seen.). — Zimmermann 1920:254.

Dytiscus porcatus Thunberg 1794:74 (Type area—"Uplandiae," Sweden. Type not seen.). —Zimmermann 1920:254.

Dytiscus punctatus Olivier 1795:12 (Type locality—not stated. Type not seen.). —Zimmermann 1920:254.

Dytiscus punctulatus ab. *maurus* Schaufuss 1882:clxxiii (Type locality—Dresden in Dresden, West Germany. Type not seen.). —Zimmermann 1920:254. —Guignot 1933:709. —Zimmermann and Gschwendtner 1938:38. —F. Balfour-Browne 1950:268.

–Zaitsev 1953:324. –Guignot 1961:857.

Dytiscus punctulatus var. *expectata* Peyerimhoff 1905:229 (Holotype female from Algeria in MNHN labelled as follows: Lac de Mouzaïa, 15 Juin 1905; v. ♀ expectatus type unique; HOLOTYPE, *Dytiscus punctulatus* ♀ var. *expectata* Peyerimhoff, examined R.E. Roughley 1981.).

Dytiscus punctulatus var. *expectatus* Peyerimhoff. **Justified emendation**. –Zimmermann 1920:254. –Guignot 1933:709. –Zimmermann and Gschwendtner 1938:38. –Guignot 1947a:242. –F. Balfour-Browne 1950:268. –Zaitsev 1953:324. –Guignot 1961:858. –Schaeflein 1971:87. –Franciscolo 1979:662.

Dytiscus punctulatus var. *laevis* Engert 1911:254 (Type locality–Corfu, Greece. Type not seen.). –Zimmermann 1920:254. –Zimmermann and Gschwendtner 1938:38. –Guignot 1961:858.

Derivation of specific epithet. – From Latin, in reference to the short sulci or grooves on the female elytra.

Diagnostic combination. – European distribution, infuscate venter (Fig.8B) and pronotum with lateral yellow margins only (Fig.2A) easily distinguish adults of this taxon.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2A; coloration of pterothoracic sterna and abdominal sterna in Fig. 8B; median lobe of male in Fig. 15B; and metacoxal processes in Fig. 21F.

Variation. – Guignot (1961:857) suggested that the completely piceous specimens of *D. semisulcatus* which Schaufuss described as ab. *maurus* is due to post-mortem changes. Pronotal colour pattern (Fig. 2A) is quite uniform in specimens that I have seen. Only very few specimens have the anterior margin of pronotum narrowly reddish or yellowish. Most specimens have the legs completely infuscate, except for anterior faces of protibia and protarsus of both sexes, and the femoral-tibial juncture of the hind two pairs of legs is marked by a rufous spot. The venter is piceous to black. Throughout most of its range, adult females exhibit sulcate elytra. Only in Palearctic Africa do non-sulcate females make up a significant proportion of population samples.

Natural history. – *D. semisulcatus* is the only species of *Dytiscus* known to overwinter in the larval stage. Blunck (1916) fully discussed the life cycle of this species in detail, indicating pupation in May. This is in contradistinction to the implication by F. Balfour-Browne (1950:270) that there is a bimodality to the life cycle in England. Balfour-Browne (1950) provides other natural history notes, as does Guignot (1933), and records the majority of teneral specimens for July, August and September. It is apparently a species of strictly fresh-water habitats.

Distribution (map, Fig. 25A). – This species ranges throughout Europe except in the north, but also occurs in northern Africa (Guignot 1961). The eastern-most record is from Turkestan, Kazakh SSSR. It occurs northward as far as southern Sweden based on locality information from specimens examined. Apparently it has been introduced into New Zealand (Ordish 1966).

Chorological relationships. – *D. semisulcatus* is broadly sympatric with most other European species of *Dytiscus*. Avaiable distribution records suggest only narrow sympatry with *D. mutinensis* and *D. lapponicus*.

Phylogenetic relationships. – I interpret members of this taxon, based on adult characters, to be the most plesiotypic of the extant species of *Dytiscus* of which females have sulcate elytra.

Material examined. – A total of 469 specimens were examined of which 242 are males and 217 are females.

3.11 **Dytiscus sharpi Wehncke, 1875**

Dytiscus sharpi Wehncke 1875:500 (Lectotype male designated here from the Wehncke collection, MNHN, labelled as follows: LECTOTYPE; SYNTYPE; Japonia [yellow label, black edging]; Thoiry; sharpi mihi.). –Zimmermann 1920:254. –Zimmermann and Gschwendtner 1938:40 –Zaitsev 1953:325.

Dytiscus validus Régimbart 1899:311 (Lectotype male designated here in the Régimbart collection, MNHN, labelled as follows: LECTOTYPE; SYNTYPE; Nagahama, July 1886, Leech; LECTOTYPE, *Dytiscus validus* Régimbart, selected R.E. Roughley.). –Zimmermann 1920:254. –Zaitsev 1953:325. **NEW SYNONYMY.**

Derivation of specific epithet. – Not specifically stated by Wehncke, but obviously named in honour of David Sharp, British entomologist. Sharp had begun to accumulate the specimens for his 1882 monograph as early as 1875 according to Severin (1892) and would have been known to Wehncke.

Diagnostic combination. – Adults of this species are most similar to those of *D. semisulcatus*. These are the only two Palearctic species with adults with only lateral yellow borders on pronotum and infuscate venter. This species is found only in the eastern part of the Palearctic Region. In addition to differences in body shape, specimens of these taxa are easily separated on the basis of tarsal character states presented in the key.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2B; coloration of pterothoracic sterna and abdominal terga in Fig. 8C; median lobe of male in Fig. 15C; and metacoxal processes in Fig. 21G.

Variation. – Too few specimens were seen to establish whether or not there are geographic patterns of variation. Few specimens have the anterior margin of the pronotum narrowly reddish. All females I have seen have sulcate elytra, but the female syntype from Wehncke's collection is sulcate basally only, the grooves only about half as long as in other specimens of the same sex. Some specimens (teneral?) have legs completely brownish-yellow and abdominal terga indistinctly maculate (Fig. 8C). Most specimens have legs and venter black.

Natural history. – I can find nothing published about the natural history of this species, nor does the scanty label data supply any information.

Distribution (map, Fig. 25B). – I have seen records for the People's Republic of China and Japan only. This species is expected to occur also in the extreme southeastern corner of the USSR.

Chorological relationships. – *D. sharpi* is broadly sympatric only with *D. delictus*, *D. dauricus* and *D. marginalis czerskii*.

Phylogenetic relationships – Members of this taxon and *D. semisulcatus* form the sister group to a Nearctic complex of species which includes *D. fasciventris*, *D. carolinus* and *D. hatchi*.

Material examined – A total of 21 specimens were examined of which 10 are males and 11 are females.

3.12 Dytiscus carolinus Aubé, 1838

Dytiscus carolinus Aubé 1838:120 (Type area—"Etats Unis d'Amérique". Type not seen.). **NEW STATUS.**

Dytiscus fasciventris, auctorum, nec Say 1824:270. —LeConte 1859:177 (*ex parte*). —Crotch 1873:408 (*ex parte*). —Wickham 1895 (*ex parte*). —Roberts 1905:106 (*ex parte*). —Blatchley 1910:231 (*ex parte*). —Zimmermann 1919:233 (*ex parte*). —Zimmermann 1920:248 (*ex parte*). —Hatch 1929:226 (*ex parte*). —Wallis 1950:51 (*ex parte*). —Hatch 1953:237 (*ex parte*). —Larson 1975:399 (*ex parte*). —Michael and Matta 1977:41.

Dytiscus new species, Young 1954:26.

? *Dytiscus fasciventris* —Folkerts 1979:346.

Derivation of specific epithet. — Not stated by Aubé, but presumably referring to the type area which is presumably the east coast of the USA in the region occupied by the states of North and South Carolina.

Notes about type material. — I acknowledge the help of Dr. F.N. Young, Bloomington, Indiana, who first pointed out the validity of this taxon. I have not seen Aubé's type(s), but detailed reference to the original description does make it clear that this is indeed the taxon to which he was referring.

Diagnostic combination. — Characters presented in the key, and the more southern distribution provide a reliable distinction between adults of *D. fasciventris* and

D. carolinus.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2C; coloration of pterothoracic sterna and abdominal terga in Fig. 8D; median lobe of male in Fig. 15D; and metacoxal processes in Fig. 21H.

Variation. – See notes under variation in the treatment of *D. fasciventris.*

Taxonomic notes. – See equivalent section in the treatment of *D. fasciventris.*

Natural history. – Dr. J.F. Matta, Old Dominion University, Norfolk, Virginia, USA, has provided unpublished collecting notes for this species in Virginia. Adults were collected at sites in which the dominant aquatic vegetation was: 1) *Ludwigia palustris* and *Lemna gemsa*, 2) *Utricularia* sp., and 3) no vegetation. Proportion of surface of ponds covered by vegetation varied from zero to complete. Each site was characterized by a large amount of detritus. Sites varied from relatively unshaded to ponds under a closed canopy.

One teneral adult male specimen (Table 4) was seen and bears the additional information: larva coll. 21.iv.73, pupa 2.v.73, ad. emerged 11.v.73. Flight records (Table 5) are two each for April and June, and one each for July and October.

Distribution (map, Fig. 25C). – Distributed in a broad U-shape, from southern New England, south along the Atlantic and Gulf Coast to Georgia, and north along the Mississippi River drainage system to southern Michigan and extreme southeastern Wisconsin, USA. As for *D. hybridus*, absence of records for eastern mountains is notable.

Chorological relationships. – *D. carolinus* is perhaps most broadly sympatric with *D. verticalis* and *D. hybridus*. Zones of parapatry with *D. fasciventris* are noted under variation and taxonomic notes in the treatment of that species.

Phylogenetic relationships. – Closely related to *D. fasciventris* (if indeed distinct, see Taxonomic Notes) and *D. hatchi*, it is the most plesiotypic of the Nearctic species whose females have sulcate elytra.

Material examined. –A total of 91 specimens were examined of which 35 are males and 56 are females.

3.13 Dytiscus fasciventris Say, 1824

Dytiscus fasciventris Say 1824:270 (Type area—"Lake Superior". Type probably lost.). —Zimmermann 1920:248 (*ex parte*). —Hatch 1929:226 (*ex parte*). —Wallis 1950:51 (*ex parte*). —Hatch 1953:237 (*ex parte*). —Wallis and Larson 1973:110. —Larson 1975:399 (*ex parte*).

Dytiscus fasciventris, auctorum, ex parte. Misidentification of *D. carolinus* Aubé, *quod vide*.

Derivation of specific epithet. – From the Latin *fascia*, band or stripe, and *venter*, belly (Brown 1956), in reference to the alternating black and yellow fasciae on the abdomen of adult specimens.

Notes about type material. – Say's type is probably lost (Larson 1975:400). Although the separation of *D. carolinus* would seem to require a type designation for one of these taxa, I hesitate to do so until it can be adequately determined that type material of *D. carolinus* is no longer extant. I am confident of assignment of these two names because of the differing type areas for these taxa.

Diagnostic combination. – Characters presented in the key and mentioned below in the section on variation should be adequate to distinguish between the three closely related species *D. fasciventris*, *D. hatchi*, and *D. carolinus*.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2D; coloration of pterothoracic sterna and abdominal terga in Fig. 9A; median lobe of male in Fig. 16A; and metacoxal processes in Fig. 21I.

Variation. – Specimens from central and northern portions of the range exhibit little variation. However, specimens occurring sympatrically with *D. carolinus* exhibit limited convergence, mainly with respect to coloration. In southern New England and adjacent areas of the USA, specimens of *D. fasciventris* are more extensively marked with reddish colour on the abdominal sterna and thus are more similar to north-eastern specimens of *D. carolinus*. As well, north-eastern specimens of *D. carolinus* are larger than more southern specimens, and therefore these two taxa are more similar in size in this region. Specimens from this area may be recognized by yellow versus infuscate metacoxal plates, females with protarsal claws shorter or subequal versus longer than protarsomere V, and shape of the median lobe of males (see key).

The other major area of sympatry, notably in Michigan, is more problematic. Most specimens from Michigan are easily assigned to one or other of the names on the basis of the characters listed above. However, a few females [Michigan, Cheboygan Co., Douglas Lake, 16.vii.1978 (UASM)] have protarsal claws longer than protarsomere V, expanded infuscation on metasternal wings, and extensive areas of red colour on the abdominal sterna. Other Michigan specimens show similar traits, especially with respect to length of female claws and sternal colour. Most of these specimens are from localities north of the known range of *D. carolinus*, but still within the potential dispersal range of this species. In Michigan, then, specimens from a few localities have character states indicative of introgression between *D. fasciventris* and *D. carolinus*.

A similar but less complex situation is indicated between *D. fasciventris* and *D. hatchi*. Pronota of eastern specimens of *D. fasciventris* lack or have very narrow anterior and posterior yellow margins. Specimens from Alberta and British Columbia have much wider anterior and posterior yellow margins. In some examples, the anterior yellow margin is 0.2 of pronotal length (Wallis 1950:51). Thus, western specimens of *D. fasciventris* are more similar to *D. hatchi* in this character, although other characters are consistently different between these two taxa. Therefore, there is a possibility that introgression is occurring or has occurred between western populations of *D. fasciventris* and *D. hatchi*.

Taxonomic notes. – *D. fasciventris* specimens have long been confused with those of *D. carolinus*, but I recognize two species. Possible introgression between *D. fasciventris* and *D. carolinus* in eastern North America, and between *D. fasciventris* and *D. hatchi* in western North America (see above) is problematic in that if all three are reproductively isolated but closely related taxa, then one would expect character displacement rather than character convergence within areas of sympatry. Despite this convergence, I retain specific level status for each of these taxa because: 1) introgression has not been conclusively demonstrated; and 2) convergence is limited to a few characters only (except in northern Michigan between *D. fasciventris* and *D. carolinus*). I do not treat *D. carolinus* and *D. fasciventris* as subspecies since: 1) the area where maximum convergence apparently occurs is north of the known range of *D. carolinus*; 2) there is no convergence in at least two characters (colour of metacoxal plates and shape of median lobe); and 3) difference in amount of character convergence between Michigan and north-eastern United States.

No evidence to suggests that introgression is occurring now. In fact, variation in degree of character convergence is suggestive of an alternative hypothesis. Much of the apparent similarity could be derived from compression, fragmentation and broad overlap of ranges which would have been necessary adjustments to, for instance, the Wisconsinan glacial epoch. Thus the apparent convergence could be indicative of Wisconsinan rather than Holocene introgression. More extensive collections of specimens from the zones of sympatry, and attempts to cross these putative specifically distinct taxa in laboratory and field situations will determine their ultimate taxonomic fate.

The major consistent differences between adult specimens of *D. fasciventris* and *D. carolinus* are given in the key to species. Other differences are length and width (Table 2), differences in form of the apex of the median lobe (compare Figs. 15d and 16a), and leg colour (generally darker in *D. carolinus*).

Wallis (1950:51) listed a number of subtle differences between specimens of *D. fasciventris* and *D. hatchi*, other than those used in the key. These are: 1) males of *D. hatchi* with elytra more distinctly punctate basally; 2) median lobe of male *D. hatchi* more linear than that of males of *D. fasciventris*; 3) infuscate markings of abdominal sterna touching the inter-sternal suture in *D. fasciventris*, as compared to isolated central blotches in *D. hatchi*; and 4) broader anterior and posterior bands of yellow of pronotum on specimens of *D. hatchi*.

Natural history. – James (1970) and Larson (1975) provide natural history notes about this species in Ontario and Alberta, Canada, respectively. Adults probably reproduce quite early in the spring and are avid predators of early spring mosquitoes. James (1970) discusses parasitoids of pupae of *D. fasciventris*.

Flight records are roughly divisible into a vernal dispersal flight from April to late June, and a post-emergence flight from July to November (Table 5). All available records for teneral specimens are for the month of July (Table 4 and Larson 1975:400).

Distribution (map, Fig. 25D). – Transcontinental in North America, from the Maritime Provinces to Vancouver

Island in Canada, this species extends southward to extreme southern Indiana, USA. The northern-most record is for Dawson City in Canada's Yukon Territory.

Chorological relationships. – Throughout its entire range, *D. fasciventris* is sympatric (at least narrowly so) with every other Nearctic species of *Dytiscus* except *D. habilis*.

Phylogenetic relationships. – *D. fasciventris* forms, in conjunction with *D. carolinus* and *D. hatchi*, a closely related assemblage of relatively recent origin, judging by the relatively small amount of structural divergence of adults, evidence of possible introgression, and geographical replacement of these taxa with only narrow zones of sympatry.

Material examined. – A total of 1,257 specimens were examined of which 610 are males, 645 females, and sex was not determined for 2 specimens.

3.14 Dytiscus hatchi Wallis, 1950

Dytiscus hatchi Wallis 1950:50 (Holotype male in CNIC, labelled as follows: Pond N. of Bethel, Washington, Apr. 21 1940; holotype male Dytiscus hatchi Wallis; holotype Dytiscus hatchi Wallis No. 5880.). —Hatch 1953:237. —Leech and Chandler 1956:323. —Larson 1975:400.

Derivation of specific epithet. – Wallis named this taxon in honour of the late Melville Hatch, noted coleopterist.

Diagnostic combination. – Character states presented in the key and distribution, supplemented by characters mentioned in taxonomic notes under treatment of *D. fasciventris* allow accurate determination of adult specimens of *D. hatchi*.

Description. – Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2E; coloration of pterothoracic sterna and abdominal terga in Fig. 9B; median lobe of male in Fig. 16B; and metacoxal processes in Fig. 21J.

Variation. – Important aspects of variation are discussed in section about variation in the treatment of *D. fasciventris*.

Taxonomic notes. – See equivalent section in treatment of *D. fasciventris*.

Natural history. – Nothing substantial is published, nor can much be inferred from label information about the natural history of this taxon. Teneral specimens are known from the month of August (Table 4). Two flight records are available for the month of July (Table 5). Because of the phylogenetic affinities of this taxon to *D. fasciventris*, it probably represents the ecological replacement of *D. fasciventris* in western North America.

Distribution (map, Fig. 25E). – The range of this species extends from British Columbia, Canada, south to California, USA. All records are from localities west of the Rocky Mountains.

Chorological relationships. – *D. hatchi* is broadly sympatric only with *D. marginicollis*. It is narrowly sympatric with its closest relative, *D. fasciventris*, in southern British Columbia, Canada.

Phylogenetic relationships. – See notes under equivalent section in treatment of *D. fasciventris*.

Material examined. –A total of 222 specimens were examined of which 107 are males, 112 females, and sex was not determined for 3 specimens.

3.15 **Dytiscus cordieri** Aubé, 1838

Dytiscus cordieri Aubé 1838:108 (Type locality - "...Boston...", Mass., USA. Type not seen). —Zimmermann 1920:246. —Wallis, 1950:51. —Hatch 1953:238. —Gordon and Post 1965:25. —Wallis and Larson 1973:110. —Larson 1975:400.

Dytiscus sublimbatus LeConte 1857:34 (Type locality - "Prairie Paso", Oregon Territory. Holotype female in LeConte collection, MCZC, labelled as follows: "Or.; D. sublimbatus Lec; Horn Coll H. 1485"). —Zimmermann 1920:246. —Hatch 1929:226. —Wallis and Larson 1973:110.

Dytiscus marginalis auctorum, nec Linnaeus 1758. **Misidentification.** Sharp 1882:641 (*ex parte*). —Ganglbauer 1892:515 (*ex parte*). —Wickham 1895:151 (*ex parte*). —Roberts 1905:106 (*ex parte*). —Csiki 1908:508 (*ex parte*). —Reitter 1908:233 (*ex parte*). —Reitter 1909:46 (*ex parte*). —Des Gozis 1910:12 (*ex parte*). —Blunck 1913:47 (*ex parte*). —Schaufuss 1913:138 (*ex parte*). —Zimmermann 1920:250 (*ex parte*). —Guignot 1933:718 (*ex parte*). —Houlbert 1934:133 (*ex parte*). —Zimmermann and Gschwendtner 1938:47 (*ex parte*) —Guignot, 1947:243 (*ex parte*). —Balfour-Browne 1950:270 (*ex parte*). —Zaitsev 1953:327 (*ex parte*). —Galewski 1971a:100 (*ex parte*). —Franciscolo 1979:665 (*ex parte*).

Derivation of specific epithet. - Obscure, but possibly with reference to the French word "cordier", meaning a rope-maker or rope-merchant. Perhaps a reference to the collector's name or occupation of the procuror of the specimens for Chevrolat in Boston.

Notes about type material. – I have not seen the type(s) of *D. cordieri*. Severin (1892) records a syntype in the Royal Museum in Brussels, Belgium. Aubé's type locality, Boston, Massachusetts, USA, is based on a single male specimen provided by Chevrolat.

Sharp (1882:773) states that he had seen the holotype, but that it was a very mutilated specimen of *D. fasciventris* Sharp wrote, "Aube's description does not agree well with this individual, or with any other species, and I think it must have been made from this individual and supplemented or corrected from another species..." This is in contrast to the statement by Aube (1838) that "...Je n'ai vu de ce Dytique qu'un seul individu..." Sharp (1882:638) used the LeConte name, *D. sublimbatus*, presumably because of this confusion over the type. After the holotype and moe specimens Aube's from Aubé's original series are studied, his concept will be better understood, and nomenclatural changes may be necessary.

LeConte's *D. sublimbatus* was described from a specimen from Prairie Paso, "Oregon Territory". I have not found this locality. The type is a nonsulcate female.

Diagnostic combination. – Distinct in North America as the only species of which adults possess obtuse apices of metacoxal lobes and a yellow venter (Figs. 21K and 9C). The only other Nearctic species with venter of adults yellow are *D. circumcinctus* and *D. alaskanus* (some specimens); members of both species have acuminate metacoxal lobes.

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3A; coloration of pterothoracic and abdominal sterna in Fig. 9C; median lobe of male in Fig. 16C; and metacoxal processes in Fig. 21K.

Taxonomic notes. – I believe most records of *D. marginalis* in North America are based on specimens of *D. cordieri*, or on mislabelled specimens. Adult *D. cordieri* are most easily distinguished from *D. marginalis* by an elongate chevron on the frons extended to the antennal bases. In addition, adult male specimens of these two taxa are easily separated on the basis of pronotal structure (not explanate in *D. cordieri*, explanate in *D. marginalis*), and shape of apex of median lobe (rounded in *D. cordieri*, Fig. 16C); with distinct apical knob in *D. marginalis*, Fig. 17C). Adult females are more similar because those of *D. cordieri* are shallowly or indistinctly explanate laterally, while those of *D. marginalis* are more distinctly explanate. Female adults are best separated by association with males and distribution. Further discussion of the confusion between *D. cordieri* and *D. marginalis* is provided within the treatment of the latter.

Variation. – There is a geographic basis to the occurrence of sulcate females. Most eastern specimens are sulcate and most western, nonsulcate. For example 59 of 67 adult females from Ontario were sulcate, while of 142 specimens examined by Larson (1975) and me from Alberta, British Columbia, Manitoba and Saskatchewan, 11 are sulcate.

Almost all adult specimens of *D. cordieri* have the distinctively elongate chevron of the frons. In a few specimens, however, this is difficult to see because of post-mortem discoloration. Once these specimens are sufficiently cleaned, it is quite distinctive.

Pterothoracic sternal coloration is predominantly yellowish. The darkest specimen seen, which is quite outside the normal range of variation, is illustrated in Fig. 9C. Infuscation is restricted to the central area of the metasternum and sutures of the sterna in most specimens.

Natural history. – Larval development is probably completed between mid-July and mid-August, since teneral adults have been collected in late July and throughout August (Table 4). I have no information about overwintering sites of adults, except one specimen from Aweme, Manitoba, 26.iv.30 (1 CNIC) "taken under logs out of water". This record could represent an overwintering site, but could just as easily indicate an example of a poor choice for a landing during dispersal. Label data indicative of dispersal is presented in Table 5. Records predominate for April in the spring and post-emergence flight takes place from July to October.

Larson (1975:401) noted that adults of *D. cordieri* occur in a wide variety of types of water body, and furthermore, that most records of *D. cordieri* are represented by individuals, with the longest series he had seen from Alberta being three specimens. Larson suggested that this was due either to low population densities or to insufficient knowledge of microhabitat of adults.

Using data from museum specimens, which has limitations, I tallied the number of adult specimens collected on a single day by a single collector, hereafter referred to as a sample. Of 335 samples from almost the entire range of the species, the average was 1.6 specimens. A similar tally for adult *D. alaskanus* yielded 202 samples averaging 3.4 specimens. The latter perhaps is more typical of *Dytiscus* adults. Less than 20 of these samples of adult *D. cordieri* were of more than five specimens, including bottle-trapped samples, and most of these are from April or from late August to early October, and were probably collected during or shortly after dispersal flight. By inference, I conclude that adults of *D. cordieri* occur at a lower population density than do those of other species.

Distribution (map, Fig. 26A). – This species is transcontinental in North America, ranging from Alaska and the Northwest Territories, south to central California and northern Colorado, with the most southern record being from Gastonia, North Carolina.

Chorological relationships. – In some part of its range, *D. cordieri* is sympatric with every other Nearctic species of *Dytiscus* except the Mexican *D. habilis*.

Phylogenetic relationships. – In my phylogenetic interpretation of *Dytiscus*, I have placed this species within the *D. dimidiatus*-group on the basis of presence of rounded metacoxal processes, rounded apex of the median lobe, and absence of a distinct knob at the apex of the median lobe. Specimens of *D. cordieri* are phenetically quite distinct from other members of the *D. dimidatus*-group and represent the only Nearctic members of the group.

Material examined. – A total of 691 adult specimens were examined of which 362 were males, 328 were females, and for one specimen sex was not determined.

3.16 **Dytiscus mutinensis** Pederzani, 1971

Dytiscus dimidiatus ab. *mutinensis* Fiori 1881:276 (Information about types below). –Zimmermann 1920:248. –Müller 1926:298. –Guignot 1933:715 (*ex parte*). –Zimmermann and Gschwendtner 1938:40. –F. Balfour-Browne 1950:285. –Zaitsev 1953:325. –Schaeflein 1971:87. –Franciscolo 1979:663.

Dytiscus pisanus var. *mutinensis*; Guignot 1931:7 (Misidentification of *D. dimidiatus*), *quod vide*.

Dytiscus mutinensis Pederzani 1971:220 (Information about types below). –Schaeflein 1973:74.

Derivation of specific epithet. – From "Mutina", the Latin name of Modena, Italy, Fiori's type locality.

Notes about type material. – Fiori's type is discussed by Pederzani (1971). Pederzani, when elevating this taxon to specific rank, retained the same epithet, presumably to provide continuity in use of this name. For his new, species-level taxon, Pederzani designated a new type specimen from Italy for which he gives the following information: "Holotypus [male symbol]: Ravenna, pineta di S. Vitale, 20.ix.1970, leg. Pederzani." It is deposited in the Museo Civico di Storia Naturale de Milano, Italy (Pederzani, 1971:222).

Diagnostic combination. – Adults of this species are best separated by characters presented in the key. Supplemental character states distinguishing it from

D. dimidiatus and *D. pisanus* are provided by Pederzani (1971).

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3B; coloration of pterothoracic and abdominal sterna in Fig. 9D; median lobe of male in Fig. 16D; and metacoxal processes in Fig. 21L.

Taxonomic notes. – This taxon has long been confused with members of *D. dimidiatus* because adults are quite similar in external features. Pederzani (1971) was the first to distinguish this taxon as being of specific rank. As such, a new holotype was needed, and a specimen was so designated by that author.

Part of the taxonomic confusion arose because non-sulcate females of *D. dimidiatus* were assigned to *D. dimidiatus* ab. *mutinensis*. Guignot's (1931, 1933) record of this aberration from France, Department of Bouches-du-Rhône, St. Rémy (1 MNHN) is such a non-sulcate female. Both *D. dimidiatus* and *D. mutinensis* have the sulcate and non-sulcate states of the elytra of females.

Franciscolo (1979:663-664) expresses reservations about the species-level separation of *D. mutinensis* and *D. dimidiatus*. As he infers, the longer metatarsomere V of male *D. dimidiatus* would be expected to have more punctures (approximately 60) than that of the shorter one of *D. mutinensis* (approximately 30), and this is one of the major differences used by Pederzani (1971) and me. Franciscolo notes that other differences between these putative species are very subtle.

I have maintained the separation of these taxa as species for the following reasons: 1) consistent, if slight, differences in shape of median lobe of males; 2) information provided by Franciscolo (1979) that specimens assignable to both taxa were taken in the same ponds; and 3) lack of intermediate specimens among the limited sample I have seen. I believe that the subtlety of differences between members of these taxa is due to recent speciation.

Variation. – I saw slight variation in external features of adults in 12 specimens of *D. mutinensis*. Of the five males examined in detail, number of punctures on the anterior surface of protarsomere V ranged between 24 and 34.

Presence or absence of the anterior yellow band of the pronotum varies, but when present, this band is quite narrow, in most less than 10% of width of lateral bands. Two of the four females from Corfu have slightly impressed grooves.

Natural history. – Pederzani (1971) notes a preference of adult specimens of *D. mutinensis* for lentic habitats with much vegetation and detrius. They occur in both open and shaded habitats, but locally. Angelini (1978) provides more detailed notes about habitats where specimens of *D. mutinensis* were collected, and adds occurrence in slowly moving water.

Distribution (map, Fig. 26B). – This species occurs throughout Italy and around the Adriatic Sea. Guignot's record from France is discussed above. I suspect that the records of this aberration from southern France provided by Thérond (1975:106) will also prove to be non-sulcate females of *D. dimidiatus*. Therefore, these latter records do not appear on Fig. 26b.

Chorological relationships. – Even though it occupies a small range, *D. mutinensis* is sympatric with all other European species except *Dytiscus lapponicus*.

Phylogenetic relationships. – I have interpretted *D. mutinensis* as the sister species of *D. dimidiatus*, both of which are allied to *D. cordieri* and *D. pisanus*.

Material examined. – A total of 13 adult specimens were examined, of which 8 were males, and 5 were females.

3.17.3 **Dytiscus dimidiatus** Bergsträsser, 1778

Dytiscus dimidiatus Bergstässer 1778:33 (Type locality – Hanau area of Hessen, West Germany. Type not seen.). –Zimmermann 1920:247. –Guignot 1933:712. –Houlbert 1934:132. –Zimmermann and Gschwendtner 1938:40. –Guignot 1947a:242. –F. Balfour-Browne 1950:285. –1953:27 –Zaitsev 1953:325. –Galewski 1971a:100. –Schaeflein 1971:87. –Pederzani 1971:222. –Franciscolo 1979:663.

Dytiscus dimidiatus ab. *mutinensis*; Guignot 1933:715 (*ex parte*).

Dytiscus pisanus ab. *mutinensis*; Guignot 1931:7.

Derivation of specific epithet. – Latin for 'halved', presumably in reference to length of elytral sulci of adult females (Fig. 3c).

Diagnostic combination. – Adults of this species are best separated by characters presented in the key.

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3C; coloration of pterothoracic and abdominal sterna in Fig. 10A; median lobe of male in Fig. 17A; and metacoxal processes in Fig. 21M.

Taxonomic notes. – For a discussion of the confusion of species between *D. mutinensis* and *D. dimidiatus* by previous taxonomists, see the equivalent section in the treatment of the former species.

Variation. – Slight variation in external features of adults was noted and consisted mostly of presence, absence and width of anterior and posterior yellow bands of the pronotum. The anterior yellow band was consistently less than 30% of the width of the lateral bands of the pronotum.

Most females have sulcate elytra. For a discussion of record of non-sulcate females, see Taxonomic notes under *D. mutinensis*.

Natural history. – Balfour-Browne (1950) stated that adults of this species are typically found in fens with occasional records from more temporary or disturbed habitats. He also gives a flight record for May and a record of a teneral specimen for September.

Pederzani (1971) implies that specimens live in both open, disturbed habitats as well as more mature ponds. Neither this species nor *D. mutinensis* are found as adults in anything but very slowly running water. Korschelt (1923, 1924) gives further details about natural history of this species.

Distribution (map, Fig. 26C). – This species occurs throughout Europe. In Scandinavia, I have no records north of about 62°N. The easternmost record is at about 41°E. I have seen specimens labelled simply "Africa" (CASC) but have not been able to find any precise locality records for Africa.

Chorological relationships. – *D. dimidiatus* is sympatric with every other species of *Dytiscus* occurring in

Europe.

Phylogenetic relationships. – See equivalent section under treatment of *D. mutinensis*.

Material examined. – A total of 305 adults were examined, of which 156 are males and 149 are females.

3.18 *Dytiscus pisanus* LaPorte Compte de Castelnau, 1835

Dytiscus pisanus LaPorte Compte de Castelnau 1835:98 (Type locality – "Pise", Italy. Lectotype, here selected – male in BMNH labelled: LECTOTYPE; SYNTYPE; Sharp coll., 1905-313;*Dytiscus pisanus* Lap., Italia [male symbol]; LECTOTYPE, *Dytiscus pisanus* LaPorte de Castelnau 1835, selected R.E. Roughley.). –Zimmermann 1920:253. –Guignot 1933:719. –Houlbert 1934:134. –Zimmermann and Gschwendtner 1938:44. –Guignot 1947a:244. –Guignot 1961:859. –Pederzani 1971:224. –Franciscolo 1979:666.

Dytiscus ibericus Rosenhauer 1856:47 (Type locality – Algeciras, Spain. Type not seen.) –Zimmermann 1920:253.

Dytiscus pisanus var. *ibericus*; –Guignot 1931:7. –Guignot 1933:719. –Zimmermann and Gschwendtner 1938:44. –Guignot 1947a:244. –Guignot 1961:859. –Franciscolo 1979:667.

Dytiscus pisanus var. *nonsulcatus* Zimmermann 1919:233 (Type locality – not given. Holotype in Zimmermann collection, ZSBS, labelled as follows: ♀; Tanger, Rolph; Type; Holotypus, Dytiscus pisanus ♀ var. nonsulcatus Zim., Staatssaml. München.). –Zimmermann 1920:253. –Pederzani 1971:219.

Derivation of specific epithet. – "Pisanus" is the adjectival form of the name of the type locality, Pisa, Italy.

Diagnostic combination. – European distribution, pronotum broadly margined with yellow on all sides, combined with rounded lobe of metacoxal process and detailed features presented in the key allow accurate determination of adult specimens. Also, the form of the median lobe of male adults is quite distinctive (Fig. 17B).

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3D; coloration of pterothoracic and abdominal sterna in Fig. 10B; median lobe of male in Fig. 17B; and metacoxal processes in Fig. 21N.

Variation. – I have seen too few specimens of this taxon to assess patterns of variation. More than half of the specimens seen have the pterothoracic sterna piceous ventrally as in Fig. 10b. Associated with this coloration in most specimens is a darkening of abdominal sterna. Conversely, those specimens with lighter pterothoracic sterna tend to be closer to uniformly yellow in ventral coloration.

Guignot (1933:720) states that the non-sulcate form is quite rare. To his list of localities for non-sulcate females, I add only Godelleta, Spain (1 MCZC). Thus, the non-sulcate form is restricted to the southern and western parts of the range (southern France, Spain, Morocco and Algeria).

Taxonomic notes. – Guignot (1933) states that certain (unnamed) authors proposed to make *D. pisanus* a variety of *D. marginalis*. He provides several minor distinctions between adults of these species, and a major difference in form of the median lobe. These distinctions, in conjunction with those presented in the key, demonstrate that two species are represented, especially when supplemented with the information that *D. pisanus* is widely sympatric with *D. marginalis*.

Zimmermann (1919) erected *D. pisanus* var. *nonsulcatus* for female forms with smooth elytra. Many authors have used *ibericus* for this form, but Pederzani (1971) examined five specimens from MNHN determined as *Dytiscus ibericus* and states that they were grooved.

Natural history. – Guignot (1933) states that adults of *D. pisanus* live in calm, clear water. However, Pederzani (1971) notes a preference for running water or for pools in stream beds.

Distribution (map, Fig. 26D). – This species has a Mediterranean distribution, but does occur as far north as 50°. The easternmost record is for the island of Crete, and the southernmost are Algeria and Morocco.

Chorological relationships. – Apparently sympatric with every other European species of *Dytiscus*. If its preference for running water is correct though, it may well occupy a distinctly different microhabitat from that of most co-occurring taxa.

Phylogenetic relationships. – The rounded apex of the median lobe indicates a close relationship to *Dytiscus mutinensis* and *Dytiscus dimidiatus*.

Material examined. – A total of 129 specimens were examined of which 50 were males and 79 females.

3.19 **Dytiscus marginalis** Linnaeus, 1758

Dytiscus marginalis Linnaeus 1758:411.

Derivation of specific epithet. – With reference to all sides of the pronotum, or alternatively, lateral edges of elytra being margined with yellow.

Diagnostic combination. – The combination of Palearctic distribution, acute but not acuminate metacoxal lobes, pronotum with yellow margin on all sides, and form of median lobe of males distinguish males of this taxon.

Taxonomic notes. – Some notes about confusion between *D. marginalis* and *D. cordieri* are presented under the treatment of the latter. Sharp (1882:641) was the first to ascribe *D. marginalis* to the Nearctic fauna based on a female specimen labelled "am. bor. int., montagnes rocheuses", and another individual "...said to be from North America, in Murray's collection." The latter record refers to a specimen of *D. cordieri*. The former specimen, provided by Castelnau, is deposited in BMNH and is a sulcate female of *D. marginalis*. I believe this specimen to be mislabelled. Similarily, I have seen the following specimens of *D. marginalis* which presumably have incorrect locality information: America (1 HNHM), "Ind." (1 CNIC), Canada? (1 MCZC), Detroit, Mich. (3 ICCM), Grand Portage, Labr. 2.vi.17 (1 ICCM), Montreal, Quebec (1 ICCM), Allegheny Co., Pa., vi.25 (1 ICCM), Quebec (1 ICCM), Ridgeway, Ont. (1 ICCM), and Toronto, Ont., vi.14 (1 ICCM). As Brinck

(1946:146) pointed out, there is little difference in form of the median lobe between eastern and western Palearctic specimens of *D. marginalis*. However, there are major differences in ventral coloration, and these colour forms are geographically vicariant. Thus, I have decided to treat *D. marginalis* as two subspecies: 1) the nominate, western Palearctic form, characterized by predominantly yellow pterothoracic sterna; and 2) an eastern Palearctic form for which the name *D. czerskii* is available and in which adults have the pterothoracic sterna appreciably marked with black or piceous. The two forms are allopatric and could represent taxa of specific level. However, differences in form of the median lobe are too slight to support such a conclusion, without additional supporting evidence. I have not seen intermediates in type of ventral coloration.

Distribution. – This ubiquitous Palearctic species, when the combined ranges of both subspecies are considered, includes most of the Palearctic region.

Chorological relationships. – The aggregate range of both subspecies of this species suggest that it is sympatric with every other Palearctic species of *Dytiscus* except possibly *D. sinensis*.

Phylogenetic relationships. – Presence of character states such as acute metacoxal lobes, margined pronotum, as well as those found in form of the median lobe of males, indicate that it is closest to *D. persicus* and *D. delictus*.

Dytiscus marginalis marginalis Linnaeus, 1758, NEW STATUS

Dytiscus marginalis Linnaeus 1758:411 (Type area - "Europae". Type not seen.). —Zimmermann 1920:249. —Müller 1926:298. —Guignot 1933:715. —Houlbert 1934:133. —Zimmermann and Gschwendtner 1938:47. —Guignot 1947a:243. —F. Balfour-Browne 1950:270. —F. Balfour-Browne 1953:27. —Zaitsev 1953:327. —Galewski 1971a:100. —Schaeflein 1971:88. —Franciscolo 1979:665.

D. marginalis, auctorum. Nearctic records are *D. cordieri, quod vide*. Misidentification.

Dytiscus semistriatus Linnaeus 1758:412 (Type area - "Europae". Type not seen.). —Zimmermann 1920:250.

Dytiscus totomarginalis DeGeer 1774:391 (Type locality not stated. Type not seen.). —Zimmermann 1920:250.

Dytiscus conformis Kunze 1812:58 (Type locality - "Leipzig". Type not seen.). —Zimmermann 1920:250

Dytiscus marginalis var. *conformis* Kunze; —Zimmermann 1920:250. —Müller 1926:298. —Guignot 1933:715. —Zimmermann and Gschwendtner 1938:47. —Guignot 1947a:243. —F. Balfour-Browne 1950:250. —Zaitsev 1953:327. —Schaeflein 1971:88. —Franciscolo 1979:665.

Dytiscus submarginalis Stephens 1828:90 (Type locatity - "taken near London, England". Lectotype male, selected here, in BMNH, labelled as follows: "LECTOTYPE; SYNTYPE; LECTOTYPE, Dytiscus submarginalis Stephens, selected R.E. Roughley").

Dytiscus circumductus Serville 1830:90 (Type locality - near Paris, France. Type not seen). Zimmermann 1920:251.

Dytiscus marginalis form *semicostata* Reineck 1921:117 (Type locality - "...in Kurland in der Misse-Niederung." Type not seen.). –Guignot 1933:715. –Zimmermann and Gschwendtner 1938:47. –Guignot 1947a:243. –F. Balfour-Browne 1950:240. –Zaitsev 1953:327.

Diagnostic combination. - The yellow pterothoracic sterna and western Palearctic distribution, in combination with the diagnostic combination of the species, are sufficient to identify adult members of *D. marginalis marginalis*.

Description. - Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3E; coloration of pterothoracic and abdominal sterna in Fig. 10C; median lobe of male in Fig. 17C; and metacoxal processes in Fig. 22A.

Variation. - As noted above, form of the median lobe of adult males varies only slightly between subspecies, and variation within subspecies is even less. Other aspects of variation include pronotal width, coloration of pterothoracic sterna, and suclate or non-sulcate elytra of females.

Males and females from higher elevations in the Pyrenees and Cantabrian Mountains have the pronota narrower than the base of the elytra. In lowland specimens, pronota are distinctly broader than elytral bases. The latter is true for lowland specimens from central Spain, and I have therefore not treated this form as subspecifically distinct. It is more likely that the change in pronotal form is due to dietary and thermal effects of cold, oligotrophic alpine lakes and ponds.

Sharp (1882) discussed a specimen, which I have seen, of *D. marginalis marginalis* with expanded dark fasciae on the abdominal sterna. This specimen is a male and the median lobe is protruding, but the apex is damaged. After detailed comparison of this specimen with specimens of other Palearctic species, I judge the specimen to belong to *D. persicus*, even though labelled as coming from Europe. Others (e.g., Zaitsev 1953) have mentioned increased infuscation of the abdominal sterna. In all specimens that I have seen there is virtually no infuscation of the abdominal venter except for very narrow infuscation along abdominal sutures ventrally (Fig.10C). Thus, adults of this subspecies are best separated from members of *D. marginalis czerskii* on the basis of lack of appreciable pterothoracic infuscation and distribution. See also notes under variation of *D. marginalis czerskii*.

Females of *D. marginalis marginalis* with non-sulcate elytra appear sporadically throughout the entire range of this taxon. There may be geographic patterns to the frequency of occurrence of the two female forms. For instance, F. Balfour-Browne (1950) states that the non-sulcate form is quite rare in Britain, or at least has been since 1828. Guignot (1933) states that the non-sulcate form occurs throughout France but is more common in central and western France. The non-sulcate form occurs throughout Italy, but Franciscolo (1979) noted a trend for it to become slightly more common in the south. For central Europe, Schaeflein (1971) characterizes the grooved female as most common, but that at certain localities in the northern and northeastern regions, the smooth form is more numerous than the grooved form. Guignot (1933) mentions that the smooth form is more common in the southern USSR, while Zaitsev (1953) apparently extends this to all of the USSR.

Natural history. – The natural history of adult and larval stages of this subspecies have been intensively studied for many years in Europe. Many of the publications are cited by Zimmermann (1920:251), and are discussed and augmented in the treatment edited by Korschelt (1923, 1924).

Distribution (map, Fig. 27A). – This subspecies is widespread in the western and central parts of the Palearctic region.

Material examined. – A total of 1382 adult specimens were examined, of which 619 were males, 762 were females, and sex of one specimen was not determined.

Dytiscus marginalis czerskii Zaitsev 1953, NEW STATUS

Dytiscus marginalis, auctorum; Sharp 1874:417. –Sharp 1882:641 (*ex parte*). –Brinck 1946:146. –Guignot 1947a:244

(*ex parte*).

Dytiscus czerskii Zaitsev 1953:328. **NEW SYNONYMY.** (Type locality - not specified, but localities listed all in Primorskij Kraj (Maritime Territory), USSR.).

Derivation of subspecific epithet. - Named in honour of A.I. Cherskii, who collected the type specimen.

Notes about type material. - I have not seen Zaitsev's type of this taxon, which, according to his preface, is deposited in the Zoological Institute of the Academy of Sciences of the USSR in Leningrad. I have, however, seen specimens authenticated by Zaitsev.

Diagnostic combination. - The infuscate pterothoracic sterna and eastern Palearctic distribution, in combination with the diagnostic combination of the species, are sufficient to identify adult members of *D. marginalis czerskii*.

Description. - Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is not shown; coloration of pterothoracic and abdominal sterna in Fig. 10D; median lobe of male in Fig. 17D; and metacoxal processes in Fig. 22B.

Variation. - I have seen too few specimens of this taxon to assess patterns of variation. Zaitsev (1953) writes that the ventral colour of *D. czerskii* is similar to that of

D. marginalis. All specimens of *D. marginalis czerskii* that I have seen have a much geater development of infuscation on the venter than is typical of more western populations of *D. marginalis*. All specimens have sternum VI broadly infuscate, and most specimens have a broad infuscate band on sternum II.

As noted under the section concerning variation in *D. marginalis marginalis*, Zaitsev implies that the non-sulcate form is the most common in the USSR. This is in marked contrast to the condition of female *D. marginalis czerskii*. Zaitsev (1953) states that all 16 females which he had seen were sulcate. I have seen an additional 8 female specimens, all of which have sulcate elytra.

Taxonomic notes. – The slight character differences mentioned by Zaitsev (1953) between *D. marginalis* and *D. czerskii* are insufficient in themselves to warrant species-level status. This is true also of differences in form of the median lobe, and I have therefore used subspecific rank for these two forms.

Natural history. – Nothing has been published about natural history of this subspecies.

Distribution (map, Fig. 27A). – This subspecies is found in the Amur and Maritime regions of the USSR, and on Japan, and is to be expected in the northeastern regions of China.

Material examined. – A total of 20 adult specimens were examined, of which six are males and 14 are females.

3.20 Dytiscus persicus Wehncke, 1876

Dytiscus persicus Wehncke 1876:52 (Type area – "Persien". Holotype female in Wehncke collection, MNHN, labelled as follows: "Persia, settente., 1862-63, Coll. G. Doria; typ; Persia; HOLOTYPE, Dytiscus persicus Wehncke, examined R.E. Roughley."). –Zimmermann 1920:235. –Zimmermann and Gschwendtner 1938:46. –Zaitsev 1953:327.

Dytiscus marginalis; Sharp 1882:641 (*ex parte*). **Misidentification.**

Derivation of specific epithet. – Named for "Persia", Wehncke's type area.

Notes about type material. – Wehncke's description indicates that he had seen only one non-sulcate female of this species from the Dohrn collection. The holotype was placed beside a large label reading "persicus mihi" in Wehncke's handwriting. The BMNH contains two other non-sulcate female specimens labelled: "Co-type; Persia, settente., 1862-63, coll. G. Doria; Sharp coll., 1905-313 [label inverted]; Ispahan. Persia. J. Doria 1862-3, persicus", the bottom label in David Sharp's handwriting. These BMNH specimens cannot be considered part of the type series of *D. persicus* because, based on Wehncke's original description, they were not seen by him, even though they are part of the same series of specimens. Sharp may have obtained the specimens from Doria. Sharp (1882) states that these specimens may be from Isfahan (=Esfahan), Iran, but does not mention the source of this information.

Diagnostic combination. – This is the only western Palearctic species other than *D. pisanus*, *D. circumcinctus* and *D. lapponicus* of which adults have transverse black fasciae on the abdominal venter. The latter two have longer metacoxal processes, while *D. persicus* and *D. pisanus* have quite separate ranges.

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is not shown; coloration of pterothoracic and abdominal sterna in Fig. 11A; median lobe of male in Fig. 18A; and metacoxal processes in Fig. 22C.

Taxonomic notes. – See notes provided under *D. marginalis*.

Variation. – I have seen only 19 specimens assignable to this name, and have therefore little information about variation. Of the ten females seen, four have sulcate elytra.

Natural history. – Unknown.

Distribution (map, Fig. 27B). – Zaitsev (1953:328) records this species from Iran, northeastern Turkey and from the southern coast of Crimea, Dagestan and Transcaucasia in the USSR. I have assigned a specimen from Narin, Afghanistan to this species.

Chorological relationships. – I have seen few specific locality records for any species from the range of

D. persicus, and cannot make a confident statement of co-occurence with other taxa. However, it may be sympatric with *D. semisulcatus*, *D. dimidiatus*, *D. marginalis*, *D. circumflexus* and *D. thianshanicus*.

Phylogenetic relationships. – Adult members of this species show characteristics indicating that *D. persicus* is related to *D. marginalis* and *D. delictus*.

Material examined. – A total of 19 adult specimens were examined, of which nine are males and 10 are females.

3.21 Dytiscus delictus (Zaitzev, 1905)

Macrodytes delictus Zaitzev 1905:28 (Type locality - Charbarovsk, Chabarovsk Kraj, RSFSR, USSR. Type not seen).

Dytiscus delictus; -Zimmermann 1920:247. -Zimmermann and Gschwendtner 1938:43. -Zaitsev 1953:326.

Derivation of specific epithet. - Not stated by Zaitzev. The latin word *delictus* means "faulted" or "failed", but the significance of this epithet is not apparent.

Notes about type material. - I have not seen type specimens of this species, but have seen specimens authenticated by P. Zaitzev.

Diagnostic combination. - Eastern Palearctic distribution, acute metacoxal lobes, and fasciate abdominal sterna distinguish adults of this taxon from those of other species of *Dytiscus*.

Description. - Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 4A; coloration of pterothoracic and abdominal sterna in Fig. 11B; median lobe of male in Fig. 18B; and metacoxal processes in Fig. 22D.

Variation. - I have seen too few specimens to assess patterns of variation.

Natural history. - Unknown.

Taxonomic notes. – Zaitzev (1905) accepted *Macrodytes* as a distinct genus, and assigned his species, *delictus*, to it.

Distribution (map, Fig. 27C). – I have seen specimens from Chabarovsk Kraj, Primorskij Kraj, and Sachalin Oblast of the eastern USSR. Zaitsev (1953) reports specimens from the same general area. This species may also occur in northeastern China and Japan.

Chorological relationships. – *D. delictus* is sympatric with *D. sharpi*, *D. marginalis czerskii*, *D. dauricus*, *D. circumcinctus*, and *D. latro*.

Phylogenetic relationships. – This species represents the eastern vicar of *D. persicus*.

Material examined. – A total of 20 adult specimens were examined, of which nine are males and 11 are females.

3.22 **Dytiscus latissimus** Linnaeus, 1758

Dytiscus latissimus Linnaeus 1758:411 (Type area - "Europae". Type not seen.). —Zimmermann 1920:242. —Guignot 1933:730. —Houlbert 1934:132. —Zimmermann and Gschwendtner 1938:35. —Guignot 1947a:247. —Zaitsev 1953:321. —Schaeflein 1971:86. —Franciscolo 1979:671.

Dytiscus amplissimus Müller 1776:69 (Type area - not stated, presumably Denmark). —Zimmermann 1920:243.

Dytiscus anastomozans Well 1781:386 (Type locality - not known to me. Type not seen.). —Zimmermann 1920:244.

Derivation of specific epithet. - This name is derived from the superlative form of Latin *latus*, meaning "broad" or "wide". It is an apt name for this taxon because of the great width of the body of adults.

Diagnostic combination. - The great width of the body and widening of the elytral epipleura are sufficient to distinguish adults of this taxon.

Description. - Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 4B; coloration of pterothoracic and abdominal sterna in Fig. 11C; median lobe of male in Fig. 18C; and metacoxal processes in Fig. 22E.

Taxonomic notes. - Most recent European workers have arranged the species of *Dytiscus* in two subgenera: the nominate subgenus, and subgenus *Macrodytes* Thomson. Members of *D. latissimus* have traditionally been placed in subgenus *Dytiscus*. The generitype of *Dytiscus*, however, is *D. marginalis*, and the group of species generally treated as belonging to *Macrodytes* should in fact be assigned to subgenus *Dytiscus*. Despite such nomenclatorial problems, it is clear that the intention of earlier authors was to isolate *D. latissimus* in a separate subgenus because of its distinctiveness I do not believe that any subgeneric distinction is necessary within *Dytiscus*, and based on phylogenetic analysis it is not warranted for members of *D. latissimus*. For further discussion of this nomenclatoral confusion, see the generic treatment.

Variation. – Non-sulcate females of *D. latissimus* are not known. This is unique among Palearctic taxa of *Dytiscus* except possibly for *D. marginalis czerskii*. However, only a few specimens of the latter taxon are known. Such a uniform condition of sulcate females suggests that females are under strong selective pressure for grooved elytra. Study of the behavioural function, and hydrodynamic importance of sulci in this species may provide the key to understanding evolution of grooved elytra among members of *Dytiscus*.

Natural history. – Guignot (1933), Zaitsev (1953), and other European authors characterize the habitat of this species as large bodies of water; that is, large ponds and lakes, although I am not sure whether or not this species occurs in open water within this habitat. Many specimens have been recorded as being collected in fish weirs.

Distribution (map, Fig. 27D). – Occurs throughout the northern portions of the Palearctic realm, except Great Britain. The southernmost record is from Yugoslavia, probably associated with long range dispersal (Apfelbeck 1904:308).

Chorological relationships. – I have few records from the far eastern Palearctic Region, and it is therefore difficut to assess areas of sympatry with such species as *D. sharpi*, *D. delictus*, *D. marginalis czerskii*, *D. thianshanicus*, *D. latro* and *D. sinensis*. The known range of *D. latissimus* indicates sympatry with *D. semisulcatus*, *D. dimidiatus*, *D. pisanus*, *D. marginalis marginalis*, *D. circumcinctus*, *D. dauricus*, *D. lapponicus* and *D. circumflexus*. It is not sympatric with *D. mutinensis* and *D. persicus*.

Phylogenetic relationships. – Members of *D. latissimus* have the metacoxal processes acuminate, but less so than more advanced members of the genus such as *D. lapponicus*, *D. circumflexus*, *etc*. However, the median lobe is without an apical knob, which I interpret as a secondary loss, which has also occurred in *D. alaskanus*. I have placed *D. latissimus* as the most plesiotypic to those taxa which have acuminate metacoxal lobes.

Material examined. – A total of 428 specimens were examined, of which 208 are males and 220 are females.

3.23 Dytiscus circumcinctus Ahrens, 1811

Dytiscus circumcinctus Ahrens 1811:67 (Type locality–not known to me. Type not seen.). –Zimmermann 1920:244. –Hatch 1929:227. –Guignot 1933:720. –Houlbert 1934:134. –Zimmermann and Gschwendtner 1938:54. –Guignot 1947a:244. –F. Balfour-Browne 1950:275. –LaRivers 1951:404. –F. Balfour-Browne 1953:27. –Hatch 1953:238. –Zaitsev 1953:331. –Gordon and Post 1965:25. –Galewski 1971a:88. –Schaeflein 1971:88. –Larson 1975:401. –Franciscolo 1979:669.

Dytiscus circumcinctus Hummel 1823:17 (Type area – "Livonie". Type not seen.). –Zimmermann 1920:245.

Dytiscus flavocinctus var. *flavocinctus* Hummel 1823. –Zimmermann 1920:245. –Guignot 1933:720. –Zimmermann and Gschwendtner 1938:54. –Guignot 1947a:244. –F. Balfour-Browne 1950:277. –Zaitsev 1953:331. –Schaeflein 1971:88. –Franciscolo 1979:669.

Dytiscus dubius Gyllenhal 1827:372 (Type locality – not stated. Type not seen.). –Zimmermann 1920:245.

Dytiscus angustatus Stephens 1828:88 (Type locality – "Bomere, Salop.",England. Lectotype male selected here from Stephens collection, BMNH, and labelled as follows: LECTOTYPE; SYNTYPE; LECTOTYPE, Dytiscus angustatus Stephens selected R.E.Roughley). –Zimmermann 1920:245.

Dytiscus ooligbuckii Kirby 1837:74 (Type locality – "Great Bear Lake River", N.W.T., Canada. Type – see Larson 1975:401.). –Zimmermann 1920:247.

Dytiscus circumscriptus Boisduval and Lacordaire 1835:300 (Type locality – near Paris, France. Type not seen.). Zimmermann 1920:245. –Houlbert 1934:134.

Dytiscus anxius Mannerheim 1843:218 (Type locality – "Sitkha", Alaska. Type not seen.). –Zimmermann 1920:244. –F. Balfour-Browne 1950:277. –Leech and Chandler 1956:323. –Wallis and Larson 1973:110. –Larson 1975:401.

Dytiscus confusus Motschulsky 1860:101 (Type area – "...dans toute la Sibérie orientale, jusqu'au Kamtschatka, et a été rapporté du fl. Amour..." Syntype male in MNHM labelled: SYNTYPE; Dytiscus confusus Mots., Dauria, [illegible], 52° [or 62°] [yellow circular label]; 1; Dytiscus [male symbol] confusus Motsch, Dauri; Museum Paris, coll de Marseul 1890; SYNTYPE, Dytiscus confusus Motschulsky 1860, examined R.E. Roughley). –Zimmermann 1920:245.

Dytiscus albionicus, auctorum, nec Motschulsky 1859:166. Misidentification of *D. marginicollis*, quod vide.

Dytiscus dauricus, auctorum, nec Gebler1832:39. Misidentification. –Zimmermann and Gschwendtner 1938: 55 (*ex parte*). –Anderson 1962: 73.

Derivation of specific epithet. –This epithet is formed from the Latin words *circum* meaning around or on all sides, and *cinctum*, girdle or belt (Brown 1956). The name possibly refers to the yellow band around the dorsal edge of the eye of adults.

Notes about type material. – F. Balfour-Browne (1950) discusses many of the taxonomic problems associated with this species. Larson (1975) provides details about the type of *D. ooligbuckii*. I examined Kirby's type series of *D. angustatus* within the Stephens collection, BMNH. A lectotype is designated above, but because of the short pins used for Stephens' specimens, these are pinned beside the lectotype. In addition, there is a sulcate female specimen which is a syntype.

As noted above, I have seen a male syntype of *D. confusus* Motschulsky. My reasons for considering this specimen to be a part of the type series are: 1) the label on the box in de Marseul's collection as discussed under the treatment of *D. dauricus*; 2) the name *D. confusus* is on this list; 3) one of the labels ("Dytiscus [male symbol] confusus Motsch., Daur.") appears to be in Motschulsky's handwriting, by comparison with handwriting samples shown in Horn and Kahle (1935-37, Plate XVI, Fig. 23, and Plate XXI, Fig. 33); and 4) Motschulsky, in his discussion of this species, implies that he had seen a number of specimens from diverse localities. I have not designated this syntype as lectotype because it is in quite poor condition, lacking its head, and having only the right foreleg complete.

Diagnostic combination. –Adults possess the following combination of character states: pronotum margined with yellow on all sides, acuminate metacoxal processes, predominantly yellow pterothoracic sterna, and eyes dorsally surrounded by narrow yellow band.

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 4C; coloration of pterothoracic and abdominal sterna in Fig. 11D; median lobe of male in Figs. 18D and 19A; and metacoxal processes in Fig. 22F.

Taxonomic notes. –Many names have been proposed for this species, presumably because it is very widespread and does exhibit a certain amount of colour and structural variation. Samples from particular localities are generally uniform in colour and size and if compared with samples from adjacent localities, then assignment is usually not difficult. Taxonomic problems arise when comparing specimens from widely separated localities. In the latter example I have consistently referred to shape of the median lobe for evidence on which to make taxonomic judgments. Median lobes shown in Figs. 18D and 19A are typical of the variation in form of the median lobe yet the specimens are from localities (Edmonton, Alberta, Canada and Berlin, West Germany) from more than half of the Holarctic Region apart. The form of the median lobes of these specimens is very similar and therefore I have assigned them both to the same taxon. Another factor which has led to a proliferation of names is the occurrence of both sulcate and non-sulcate females in most populations of *D. circumcinctus*. Most early workers considered the two forms to be representative of separate taxa (see Blunck 1913 for discussion).

Variation. – As noted above there is very little variation in form of the median lobe of male specimens from throughout the entire, Holarctic range of *D. circumcinctus*. One of the major features of variation in the median lobe of adult males is positive correlation between size of specimens and length of the median lobe. Increased or shortened length of the median lobe does not significantly affect shape of the apical portion of the median lobe.

Colour of pterothoracic sterna of adults is predominantly yellow in all specimens seen. Some specimens become discolored by breakdown of fat body and other viscera but without exception these conform to the generalized pattern once thoroughly cleaned.

The majority of specimens of *D. circumcinctus* which I have seen from the Nearctic region are from western Canada and adjacent areas. Within these areas, there is some suggestion of a geographic pattern to relative frequency of elytral sulcation of females. For instance, of 309 females from Alberta, Manitoba, Northwest and Yukon Territories, Saskatchewan, and North Dakota, only 33 or 11% are sulcate. The number of specimens from other areas is much smaller, but of 28 females from Alaska, British Columbia, and Washington, 22 or 79% are sulcate.

Guignot (1933:722) and F. Balfour-Browne (1950:277) state that specimens of *D. circumcintus* are rarely collected in France and Great Britain respectively. Of those adult females collected, they mention that sulcate specimens are scarce. Guignot writes that sulcate specimens are more common in Sweden. Available information supports his claim: of 73 females from Sweden, 64 or 88% are sulcate, and of 87 females from Finland, 65 or 75% are sulcate. In these areas, *D. circumcinctus* is more commonly collected than it is in France and Great Britain. Interestingly, Zaitsev (1953:354) states that sulcate and non-sulcate females occur in about equal abundance in the U.S.S.R., but does not mention whether he noted a regional disparity in dimorphism. He also records it as the commonest species of *Dytiscus* in the U.S.S.R.

In summary, within the western portions of the Palearctic region, specimens of *D. circumcinctus* are more scarce southward, but of these, non-sulcate females make up a greater proportion. Within North America, there is a similar trend in abundance, but most records of non-sulcate females are from east of the Rocky Mountains, with sulcate females predominating to the west. These trends are only preliminary, but suggest differences in dispersal rates and sources of fauna (*e.g.* western Nearctic populations may be derived from Russian fauna *via* Beringea), or of physiological-genetic properties of non-sulcate females, or a combination of both features. Further information and investigation is warranted to achieve further understanding of the pattern.

Natural History – Most of the comments presented below refer to my own collecting experiences in western Canada, label information from specimens examined, and some literature references. As more detailed collecting notes, natural history studies, larval taxonomy and similar types of information become available, they will provide an interesting and informative comparison against, in particular, the seeming structural uniformity of adult *D. circumcintus* throughout its range.

Larson (1975:402) noted the broad range of habitats in which he had collected adults of *D. circumcinctus* within Alberta. My own collecting experience suggests that this observation is true for most of western Canada, and can extend Larson's range to highly alkaline or saline habitats. Galewski (1971b) similarly recorded a wide ecological valence for this species in Poland. However, Guignot (1933:722) implies that in France *D. circumcinctus* is restricted to cold clear aquatic habitats, and F. Balfour-Browne (1950:278) records it primarily as a locally distributed inhabitant of fens in Britain. A wide habitat range would provide an adaptive advantage for this species, and presumably forms part of the reason for its Holarctic distribution pattern. Nevertheless, in certain areas, such as France and Great Britain, its habitat diversity may be curtailed by any number of features (*e.g.* local competition).

Galewski (1964) records a specimen of *D. circumcinctus* being taken from forest litter in Poland during winter. An adult male that I collected in Edmonton, Alberta on 23.v.79 was found under a log on the south shore of the North Saskatchewan River ravine. Each year, this north-facing slope near the river is one of the last areas to lose snow cover, and temperatures are kept low because of the nearby ice on the river. I therefore suspect that this specimen overwintered at that particular site. Larson (1975:402) reported taking specimens through the ice in February. Thus, these few preliminary data suggest that adult specimens of *D. circumcinctus* may overwinter either on land or in water.

Galewski (1971b) discusses early season occurrence of this species in temporary pools where it feeds extensively before moving on to more permanent habitats for reproduction. Available flight records (Table 5 and Larson 1975) suggest one peak of dispersal in April and May and another in September and October. The majority of teneral specimens seen by Larson (1975) were from July, and in Table 4 there is one each for May, June, August and September. This variation may well indicate local topographic differences in habitats, such as availability of prey, water temperatures, *etc*.

Distribution. (maps, Figs. 27E and 27F) – This species is widespread within the Holarctic Region. In North America it is transcontinental, with records from Maine to Alaska. It occurs as far south as North Carolina, and I have taken it at tree-line in Canada's Yukon Territory. In the Palearctic region it ranges from Norway and Great Britain south to Italy (Franciscolo 1979:69) and Bulgaria (Guéorguiev 1958) and westward throughout the region. I have been unable to find records for Spain excluding the Pyrenees. It is apparently less commonly collected in the southern portions of its range.

Chorological relationships. – In some parts of its range, *D. circumcinctus* is sympatric with every other species of *Dytiscus* except *D. habilis* in the Nearctic Region, and, in the Paleartic, *D. sinensis*.

Phylogenetic relationships. – Adults of *D. circumcinctus* possess acuminate metacoxal processes and therefore belong to one of the more advanced grades within *Dytiscus*. The median lobe has an apical knob which has well-developed sensory pores, but the median lobe is not sinuate laterally. These synapotypic character states define the relative position of *D. circumcinctus* adequately, but the exact sister group relationship of the species is more problematic. The only character I could find to separate the more advanced members of this clade from *D. circumcinctus* is the relatively abrupt bend in the lateral ridge of the median lobe of advanced members, compared to the evenly curved lateral ridge of the same structure in members of *D. circumcinctus*. I believe this to be a relatively weak character, and thus the hypothesized sister group relationship may change as new characters are found and incorporated into the analysis. Members of *D. latissimus*, *D. alaskanus* and *D. circumcinctus* are very difficult to place in the cladogram. The two former species have probably lost the apical knob of the median lobe secondarily.

Material examined. – A total of 1470 specimens of *D. circumcintus* were examined: 283 males and 337 females from the Palearctic realm, and 351 males, 381 females and 18 specimens of undetermined sex from the Nearctic realm.

3.24 *Dytiscus alaskanus* J. Balfour-Browne, 1944

Dytiscus parvulus Motschulsky 1852:77 (Lectotype male designated here, in UMHF, labelled as follows: LECTOTYPE; SYNTYPE; Kadjak; Holmberg; *Dytiscus parvulus*, Ménétr., Kadjak; LECTOTYPE, *Dytiscus parvulus* Motschulsky 1852, designated R.E. Roughley; *Dytiscus alaskanus* J. B.-B. det. R.E. Roughley 1982) *nec* Müller 1776:73. —Zimmermann 1920:253. —Hatch 1929:227. —Brown 1930:237. —Wallis and Larson 1973:110. —Larson 1975:404.

Dytiscus alaskanus J. Balfour-Browne 1944:356. —Larson 1975:404.

Dytiscus ooligbuckii, J. Balfour-Browne 1949:1961. —Gordon and Post 1965:25.

Dytiscus oolibuckii, Hatch 1953:238.

Dytiscus ooligbukii, Anderson 1962:73 *nec* Kirby 1837:74. —Larson 1975:404.

Dytiscus ooligubuckii, Kirby 1837:74. **Misidentification** of *D. circumcinctus*, *quod vide*.

Derivation of specific epithet. — The name of this taxon was proposed in honour of the State of Alaska, U.S.A., where it is abundant, and which contains the type locality of *D. parvulus*, for which *alaskanus* is a replacement name.

Notes about type material. — The type series of *D. alaskanus* in UMHF consists of six specimens: five males and one female. The female is non-sulcate. The type locality, Kodiak Island, is the western-most record I have for this species. All specimens have at least sterna II, III and VI with transverse dark fascia, and most, including the lectotype, have narrow markings on sterna IV and V.

Diagnostic combination. – Adults of *D. alaskanus* are known only from the Nearctic region. Only three species within the Nearctic region have acuminate metacoxal processes: *D. circumcinctus*, *D. alaskanus* and *D. dauricus*. Specimens of *D. alaskanus* with a predominantly yellow venter are most easily separated from *D. circumcinctus* by absence of a yellow ring around the eye dorsally, by the fusion of inter-sulcal ridges apically on sulcate females (compare Figs. 4C and 5A). Specimens of *D. alaskanus* with fasciate abdominal sterna are most similar to specimens of *D. dauricus*, and are best separated by the characters presented in the key.

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5A; coloration of pterothoracic and abdominal sterna in Fig. 12A; median lobe of male in Fig. 19B; and metacoxal processes in Fig. 22G.

Taxonomic notes. – Larson (1975:404) provides a detailed history of the long, confused history of the nomenclature of this taxon.

Variation. – Larson (1975:404) provides notes about variation of this taxon within the province of Alberta, and therefore I confine this discussion to other geographic areas and to variation of some taxonomically important characters. Further discussion is provided in the treatment of *D. dauricus*.

Colour of pterothoracic sterna varies geographically. Most specimens of *D. alaskanus* observed from British Columbia, Newfoundland, Northwest and Yukon Territories have completely yellow venters, whereas the majority of specimens from intervening localities have at least some degree of infuscation. The median lobe of males of all these specimens is similar to that shown in Fig. 19b.

Larson (1975:404) mentions only one Alberta locality, near the Northwest Territories border, for non-sulcate females, and in excess of 99% of our combined samples are sulcate. Throughout most of its range, females of *D. alaskanus* are consistently sulcate, and where non-sulcate females do occur, they make up only a very small proportion of the total. The areas for which I have seen non-sulcate females, and the percentage of the total number of females seen from that geographic area (localities for non-sulcate females in parentheses) are as follows: British Columbia – 5 of 56 or 9% (Kamloops area, Summit Lake, and Mile 627 on Alaska Highway); Manitoba – 3 of 13, or 23% (The Pas); Saskatchewan – 1 of 6, or 7% (Saskatoon); Ontaria – 1 of 11, or 9% (Toronto); Colorado – 5 of 20, or 25% (Breckenridge and Science Lodge W., both in Summit Co.); Northwest Territories – 4 of 15, or 27% (Ft. Smith, Reindeer Depot, and Simpson Islands in Great Slave Lake); Alaska and Yukon

Territory – 12 of 34, or 35% (Ft. Yukon, Kodiak and Fairbanks; Mile 629 and 681 on Alaska Hwy., Chappie Lake, Von Wilczek Lake, Watson Lake, and Whitehorse). As suggested by Larson (1975), this elytral form is more common in the northwestern postion of the range of *D. alaskanus*. It is interesting, but as yet unexplained, that the co-occurring *D. circumcinctus* shows the reverse pattern over much of the same area (*i.e.* non-sulcate form predominant). Low level occurrence of non-sulcate females in other widely separated areas such as Ontario and Colorado is perhaps associated with dispersal, but possibly also independent loss of sulcation within these areas. None of the non-sulcate females is provided with label data giving precise habitat, and therefore the possibility of an ecophenotypic response cannot be ruled out.

Natural history. – Members of *D. alaskanus* are collected in very large numbers at various localities in western Canada. Many bottle traps left in George Lake, near Busby, Alberta, for two days yield 10 to 15 specimens per bottle, and have taken up to 35 specimens. Most localities where net-collecting has yielded only one or two specimens have produced many times this number when bottle traps were used subsequently. This confirms the observation made by Larson (1975) that adults are often numerically abundant at particular localities.

In northwestern North America, members of *D. alaskanus* have been collected from permanent ponds and lakes in prairie, aspen parkland and boreal forest. Specimens of *D. alaskanus* overwinter in bodies of water such as George Lake and are active quite early in the spring, often before the ice is off the lake. I have observed copulating pairs from mid-April to early June at this locality. Favoured oviposition sites are plants such as *Scirpus* and *Typha*. Held in captivity for a week to ten days, with a single plant available for oviposition, two or three females reduce a plant to shreds by constant slitting of the leaves and stem with the ovipositor. During this time, individual females lay up to 40 eggs within the plant tissue. It is not known whether females lay a similar number of eggs under field conditions, but the above number may be conservative, because availability and quality of oviposition sites, as well as quality of food is greater in the field than it is possible to provide in the laboratory.

Larval development in natural conditions is probably dependent on amount and type of food available, and on water temperature. For instance, most teneral specimens were collected in August, but in seasonally more advanced and warmer areas such as Kamloops, British Columbia, teneral specimens were collected in late June (Table 4). Larson (1975) records a teneral specimen as late as mid-October.

Some dispersal occurs in spring (Table 5) and perhaps again in autumn. It is interesting that the number of flight records is so low, given local abundance of this species throughout its range.

Distribution (map, Fig. 28A). – This species is transcontinental in North America with records from Newfoundland to Alaska. The southern limit of *D. alaskanus* is represented by an isolated population in south-central Wyoming and adjacent areas of Colorado. Most records are from south of tree-line, but some scattered records indicate possible extension onto tundra habitats.

Chorological relationships. – The range of *D. alaskanus* overlaps that of every other Nearctic species except *D. habilis* and *D. carolinus*.

Phylogenetic relationships. – As with *D. latissimus*, placement of *D. alaskanus* in the phylogenetic analysis is considered provisional because, in dorsal view, the median lobe of males of both species lack a distinct apical knob. In males of *D. alaskanus*, however, the knob is visible in ventral view, and therefore is most likely an example of reduction from the well differentiated state, unlike the condition found in *D. latissimus*. Members of *D. alaskanus* and *D. dauricus* may represent a sister pair of species, but I have been unable to find a synapotypic character state linking them.

The more advanced members of *Dytiscus*, as shown in the cladogram, are united by having the median lobe of males sinuate laterally. This is a condition absent from *D. alaskanus*. The lack of an apical knob in dorsal view and the absence of lateral sinuation of the median lobe could be part of the same evolutionary step. A shortening of the apical portion of the median lobe may have brought about changes in both character states simultaneously.

Material examined. – A total of 661 adult specimens were examined and the label information recorded from these. Of these, 387 are males and 274 are females. In addition, long series of this species from George Lake, Alberta were examined but the label information not recorded. The total number of adult specimens examined is thus in excess of 2000

3.25 *Dytiscus* *dauricus* Gebler, 1832

Dytiscus dauricus Gebler 1832:39 (Type area – "le district des mines de Nertschinsk, dans la Sibérie orientale". Lectotype male selected here from Marseul collection, MNHM, labelled as follows: LECTOTYPE; SYNTYPE; *Dytiscus* *Dauricus* Gebler, Sib. or. 62; Dytiscus dauricus Gebl., Sib. or.; [indistinguishalbe mark similar to "q"]; Lectotype, *Dytiscus* *dauricus* Gebler selected R.E. Roughley). –Zimmermann 1920:247. –Hatch 1929:227. –Brown 1930:237. –Hatch 1933:11. –Zimmermann and Gschwendtner 1938:55. –Brinck 1946:154. –J. Balfour-Browne 1947:452. –Hatch 1953:238. –Zaitsev 1953:331. –Leech and Chandler 1956:323. –Wallis and Larson 1973:110. –Larson 1975:402.

Dytiscus confluens Say 1834:440 (Type area – Maine. Type probably lost.).

Dytiscus franklinii Kirby 1837:77 (Type area – "Lat.65°", boreal North America. Type – see Larson 1975:403.). –Zimmermann 1920:247.

Dytiscus dauricus var. *franklini*, *auctorum*. **Unjustified emendation** of *D. franklinii* Kirby 1837. –Zimmermann 1920:247. –Zimmermann and Gschwendtner 1938:55. –Zaitsev 1953:354.

Dytiscus confluentus LeConte 1850:212. **Unjustified emendation** of *D. confluens* Say.

Dytiscus ooligbuckii, *sensu* LeConte 1850:212 *nec* Kirby 1837, *quod vide*.

Dytiscus ventralis Motschulsky 1855:79 (**New species** for *D. ooligbukii*, *sensu* Mannerheim 1852:303 *nec* Kirby 1837. Type locality – "Tschishlkath", near present day Skagway, Alaska. Type not seen.). –Zimmermann 1920:255. –Zaitsev 1953:331. –Larson 1975:403.

Dytiscus dauricus var. *ventralis* Motschulsky. –Zimmermann 1920:247. –Zimmermann and Gschwendtner 1938:55.

Dytiscus frontalis Motschulsky 1859:489. **Nomen nudum.** J. Balfour-Browne 1946:356.

Dytiscus frontalis Motschulsky 1860:101 (Type locality – "Kamtschatka", Alaska. Type not seen.) *nec* Marsham 1802. –Zimmermann 1920:248.

Dytiscus vexatus Sharp 1882:643 (Type area – Russian America. Type – see Larson 1975:403). –Zimmermann 1920:255.

Dytiscus dauricus var. *obscurus* Gschwendtner 1922:93 (Type locality – "Berisovka in Transbaikalien", USSR. Type not seen). Zimmermann and Gschwendtner 1938:56. – Zaitsev 1953:354.

Dytiscus amurensis J. Balfour-Browne 1944:356. **New name** for *D. frontalis* Motschulsky 1860 *nec* Marsham 1802.

Derivation of specific epithet. – Named for 'Dauria', a region in eastern Asia east of Lake Baikal (now divided between the U.S.S.R. and China), which includes the type locality.

Notes about type material. – Three sources of information were used as the basis for selection of the above lectotype of *D. dauricus*. First, a male specimen of *D. dauricus* in BMNH is labelled "Siberia; Sharp coll., 1905-313 [inverted label]; Siberia or. [inverted yellow label]; Dytiscus dauricus according to a type in de Marseul's coll." The last label is in David Sharp's handwriting. Second, Horn and Kahle (1935-1937) state that the collection of F.A. von Gebler was transferred to the René Oberthür collection in MNHM, as was that of S.A. de Marseul. Third, in de Marseul's collection is a box-label which reads "Communiqué à M. Sharp par M. Lewis le 8 1876" and in the following list is the name *D. dauricus*. From this information, I have inferred that this specimen is part of Gebler's material and available for designation as lectotype.

Diagnostic combination. – In the Nearctic region adults of only *D. dauricus* and *D. alaskanus* possess acuminate metacoxal processes and fasciate abdominal sterna. Members of these two taxa are best separated by the characters presented in the key to adults of the Nearctic region. In the Palearctic region, *D. dauricus* occurs abundantly only about as far west as the Lake Baikal region, although there is one record for Yining, China at 81°E. This distribution, in combination with fasciate abdominal sterna, and acuminate but not spinose metacoxal processes will separate members of *D. dauricus* from other congeners in this area.

Description. – Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5B; coloration of pterothoracic and abdominal sterna in Fig. 12B; median lobe of male in Fig. 19C; and metacoxal processes in Fig. 22H.

Taxonomic notes. – Larson (1975) discussed most of the taxonomic problems associated with *D. dauricus*. Many names have been proposed for this taxon, in part because in most collections it is represented by only a few specimens, and if the specimens are from widely separated geographic localities they may appear to represent different taxa, especially if characteristics of the male median lobe are excluded. Also, and perhaps correlated with the above, authors' concepts of this taxon have been poorly communicated over the years, and this has led to confusion concerning the naming of specimens.

Variation. – As noted under the treatment of Measurements (see also Table 2), there is a wide range in total length and associated measurements of the specimens seen of this species. However, specimens collected by bottle trap (Table 1) show a consistent size and are on average larger than those collected with dip nets. This sugggests a size bias associated with collecting technique. As more series of bottle-trap collected specimens become available for study, it will be valuable to test them against net collected specimens from the same geographic area.

The predominantly yellow pterothoracic and abdominal sterna are consistently marked with infuscation in the material at hand. The mode of this pattern is darker than that of *D. alaskanus*, but the variation shown in the latter eliminates ventral colour pattern as a useful taxonomic character, except on a regional basis. In certain geographic areas, population samples have a majority of specimens with, for instance, expanded infuscation of metathoracic 'wing' (*e.g.* Fig. 12B left) combined with more yellow abdominal sterna (*e.g.* Fig. 12B right). I have seen too few samples of sufficient numbers to find a pattern in this variation, and indeed, there may not be one. In general, darker specimens predominate and increased infuscation of any one sternum is correlated positively with increased infuscation of other sterna.

An important feature unique to females of *D. dauricus* is the distinct disjunction between the planes of the clypeus and the frons at the fronto-clypeal suture. The frons is markedly recessed from the clypeus (Larson 1975:403). Some female specimens of *D. alaskanus* show a slight planar disjunction in this area, and this is marked in some teneral specimens. Once specimens of both taxa have been seen, however, the difference in degree is sufficient to allow reliable use of this character for separation of female members of these taxa.

Another character used to distinguish between females of *D. alaskanus* and *D. dauricus* is arrangement of the inter-sulcal ridges at the apex of the elytron. Character state differences are presented in couplet 13 of the key to

Nearctic species. I have seen no exceptions to this dichotomy, except where elytra have been malformed, presumalbly during eclosion from the pupal cell.

Of the 41 female specimens seen from the Palearctic region, 13, or 32%, show no trace of elytral sulci, 27 are distinctly sulcate, and one specimen has the sulci only lightly impressed. From the Nearctic region, 315 specimens were available for analysis. Distribution of sulcate and non-sulcate females from North American localities is given in Table 6. These data are presented in a northwest to southeast direction. While it will be more compelling when more specimens become available for study, these preliminary numbers suggest three areas of occurrence of non-sulcate females: 1) Alaska, Yukon and Northwest Territories, Ontario, and the western Provinces of Canada, 2) Newfoundland, and 3) high altitude sites in Colorado and Wyoming. These localities are just as suggestive of development of the non-sulcate form in refugia (*i.e.* Beringia, Newfoundland, and alpine Colorado and Wyoming) as they are of environmental influence on proportion of non-sulcate females. The latter scenario is somewhat weakened when it is considered that samples of *D. dauricus* from presumably similar habitats in California, Idaho, Montana, Nevada and Utah contained no non-sulcate female specimens. Both hypotheses are weakened by the low proportion of non-sulcate females in Alaska and Yukon Territory.

Natural history. – Larval development of *D. dauricus* is completed by late July to early August in Alberta and Minnesota, as teneral specimens from the first half of August were seen by Larson (1975) and me (Table 4). This species seems to prefer permanent pond or lake habitats, and these are usually associated with some amount of tree cover (Larson, 1975).

Available flight records are for April, July, September and October (Larson, 1975, and Table 5). This species may overwinter in the permanent habitats which they inhabit because specimens were caught in bottle traps at George Lake near Busby, Alberta in late April, 1982, when the margins of the lake were ice-free, but most of the lake was still frozen. At this locality, it occurs at a much lower density than *D. alaskanus*.

Distribution (maps, Figs. 28B and 28C). – This Holarctic species ranges from Newfoundland westward to Alaska, and occurs sporadically on the Aleutian Islands. In North America, most localities are from south of tree-line, but certain localities in northern Labrador, Ontario and Manitoba probably indicate that it occurs in tundra ponds. The range of *D. dauricus* extends southward along the western mountain ranges in Colorado and California and may occur in alpine and sub-alpine ponds in these areas. In the Palearctic region, most records are from east of Lake Baikal. The most southern and western record is for Yining, China.

Chorological relationships. – In North America, this species is sympatric with every other Nearctic species except *D. habilis* and *D. carolinus*. In the Palearctic it is sympatric with *D. sharpi*, *D. marginalis czerskii*, *D. delictus*, *D. circumcinctus*, *D. lapponicus lapponicus*, *D. latro* and possibly *D. latissimus*.

Phylogenetic relationships. – The robust form and markedly curved lateral margins of the median lobe of males of *D. dauricus* indicate close relationship of this taxon to *D. lapponicus*, *D. circumflexus*, *D. thianshanicus*, *D. latro* and *D. sinensis*. Unlike these taxa, however, adults of *D. dauricus* do not have a spinose metacoxal process.

Material examined. – A total of 768 adult specimens of *D. dauricus* were examined. From the Palearctic realm were 27 males and 41 females, and from the Nearctic realm, 382 males and 336 females.

3.26 **Dytiscus lapponicus** Gyllenhal, 1808

Dytiscus lapponicus Gyllenhal 1808:468.

Derivation of specific epithet. – Latin, referring to the type locality, Lapland.

Diagnostic combination. – The combination of Palearctic distribution, acuminate metacoxal lobes, pronotum with very broad yellow margins on all sides and elytra predominantly yellow with rows of black dots easily distinguish members of *D. lapponicus*.

Taxonomic notes. – I have arranged *D. lapponicus* in two subspecies: widespread nominate subspecies, and another restricted to the Italian Alps, for which the subspecific epithet *disjunctus* is available. The form of the median lobe of both subspecies is quite similar but there is a major difference in coloration of the prothoracic disc in the material I have seen (see couplet 13 of key to Palearctic species). I have chosen to treat these named forms as a subspecies because: 1) they are allopatric; 2) other specimens of *D. lapponicus* from latitudes near or as far south as that of *D. disjunctus* (*e.g.* France, Germany and U.S.S.R) do not exhibit its characteristics; and 3) distinctiveness of both groups judging from specimens I have seen. On the basis of colour characteristics studied, each specimen was easily assigned to one or the other subspecies, and subsequent use of geographic criteria showed this to be correlated. Other colour characteristics of

D. lapponicus disjunctus not used in the key but perhaps correlated with reduced infuscation of the pronotum are greatly expanded yellow band around eye (more than 0.5 width of eye) and posterior extension and expansion of chevron such that it appears hour-glass shaped but with anterior portion wider. Other character differences are discussed by Zimmermann and Gschwendtner (1938:50).

Many Palearctic autors have commented on this form and most have suggested it to be an aberration. Below, I present a brief, selected history of the taxonomic treatment of this form.

Seidlitz (1887:111) accepted *D. disjunctus* as valid at the level of species. Zaitzev (1908) states that recognition of the form *disjunctus* as an alpine "race" is unjustified because he had seen specimens with similarly coloured pronota from northern Russia. Holdhaus (1912:423) states that *D. lapponicus* occurs in the typical or nominate form at La Grave, Isére (now in Dep't. Hautes-Alpes, France). Guignot (1933:726, 1947:246) presents records for *D. lapponicus* ab. *disjunctus* from Meyrannes near Barcellonette (Dep't. Basses-Alpes, France) and "lac du col de Lauzanier". Interestingly, Guignot, in the former reference, records La Grave as a locality for the nominate form (perhaps following Holdhaus, above) but in later work suggested it as a locality for ab.*D. disjunctus* without providing an explanation for the change. Brundin (1934:252), citing earlier authors, gives, in addition, records for

Mt. Cenis (Dep't. Savoie, France) and Simplon (Canton Valais, Switzerland). All of these localities are relatively close to the type locality of *D. lapponicus disjunctus*, but are on the northern and southwestern portions of the watershed of the Alps, whereas the type locality of *disjunctus*, Lago della Magdallena, is on the southern portion of the watershed. Re-examination of these specimens is very important. Because of the problems associated with the Guignot records, I have treated them all as belonging to the nominate subspecies. Also, I do not believe that the concept of this taxon has been well communicated among coleopterists within the region; specimens are not numerous and are restricted to only a few museums. I believe that area of collections was used previously for determination, rather than other characters. If these records do represent the nominate subspecies, then they must represent dispersal records from other areas (*e.g.* Germany) or at least be remnants of a different colonization of the Alps from that which gave rise to *D. lapponicus disjunctus*.

Zimmermann (1919:233) and Zimmermann and Gschwendtner (1938:50) cite *D. disjunctus* as an example of an inbred "race" formed by extreme geographic isolation.

F. Balfour-Browne (1950:238) suggests that the main diagnostic feature of *D. disjunctus* is fragmentation of the pronotal infuscation and that Scottish specimens of the nominate form showed evidence of an "elementary stage" of development of this character state. He therefore judged

D. disjunctus to represent a simple aberration. Zaitsev (1953:329) states that *D. disjunctus* is a psychrophilic form as he has seen specimens from Leningrad. I have not seen Zaitsev's specimens. As stated above, the paucity of available specimens may have influenced Balfour-Browne's and Zaitsev's concepts of *D. lapponicus disjunctus*. If they believed that it is only characterized by fragmentation of the infuscated portion of the pronotal disc, then they could have been misled by variation within *D. lapponicus lapponicus*.

The infuscated portion of the pronotum of specimens of the nominate subspecies does exhibit variation in width, sinuation and fragmentation, but I have seen no extralimital specimens showing character states similar to that of members of *D. lapponicus disjunctus*. Furthermore, even if this character state is demonstrated to occur in other populations, it cannot be inferred that subspecies status in invalid – only that further analysis and characters are needed.

Distribution (map, Fig. 28D). – This is a species of more northern distribution than other Paleartic species. It occurs sporadically in southern Europe, usually associated with montane, or at least cold, oligotrophic habitats. It is more common in northern Europe and is known from throughout the U.S.S.R. I have seen no reliable records for North America.

Chorological relationships. - Areally, the combined range of both subspecies suggests sympatry with most Plaearctic species except *D. sharpi*, *D. persicus* and *D. sinensis*, and possibly *D. delictus*. Differences in preferred habitat suggest that co-occurrence within habitats (or effective sympatry) could happen with *D. marginalis*, *D. circumcinctus*, *D. dauricus*, *D. latro* and *D. thianshanicus*.

Phylogenetic relationships. - Presence of acuminate metacoxal processes, sinuate lateral margins of median lobe of male, with distinct sensory-type pores on apical knob indicate close affinity with *D. thianshanicus*, *D. latro* and *D. sinensis*.

Dytiscus lapponicus lapponicus Gyllenhal 1808, NEW STATUS

Dytiscus lapponicus Gyllenhal 1808:468 (Type area - "habitat in aquis Lapponiae". Type not seen). —Zimmermann 1920:248. —Guignot 1933:48. —Houlbert 1934:134. —Zimmermann and Gschwendtner 1838:34. —F. Balfour-Browne 1953:27. —Zaitsev 1953:351. —Schaeflein 1971:88.

Dytiscus borealis Motschulsky 1860:101 (Type area - "Sibérie". Type not seen.).

Dytiscus septemtrionalis Gyllenhal 1827:373 (Type area - "Habitat in Finlandiae aquis". Type not seen.).

Dytiscus lapponicus var. *septentrionalis*. Unjustified emendation. —Zimmermann 1920:249. —Guignot 1933:723. —Houlbert 1934:134. —Zimmermann and Gschwendtner 1938:48.

–F. Balfour-Browne 1950:280. –F. Balfour-Browne 1953:27. –Zaitsev 1953:351. –Schaeflein 1971:88.

Diagnostic combination. – The broad pronotal infuscation and distribution which excludes the Italian Alps, in conjunction with the diagnostic combination of the species, are sufficient to identify adult members of *D. lapponicus lapponicus*.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5C; coloration of pterothoracic and abdominal sterna in Fig. 12C; median lobe of male in Fig. 19D, E; and metacoxal processes in Fig. 22I.

Variation. – This is a relatively varied taxon, but the limits are defined and identification is usually easy because of several unique features. With respect to diagnostic features, pronotal infuscation is somewhat varied (see Taxonomic notes under *D. lapponicus*). The width of this infuscation is at most subequal to that of the width of an anterior or posterior yellow band. The anterior and/or posterior margins of the band are sinuate in some specimens. Some specimens have the pronotal infuscation arranged in three or more blocks by longitudinal incursions of yellow.

F. Balfour-Browne (1950:281-282) noted the trend for more northern samples of *D. lapponicus lapponicus* to have a greater proportion of non-sulcate females than more southern populations. Unfortunately, he does not provide relative proportions of sulcate and non-sulcate females for the Scottish and Irish samples that he studied. Other available data also suggest this trend. Guignot (1933:726) states that the non-sulcate form does not occur in France. Horion (1941:439-440) does not mention the varietal name used for non-sulcate females (as he does for other species with dimorphic females) as occurring in Germany, although I have seen a few specimens of ungrooved females labelled only "Germania". Of 28 female specimens seen from Prussia and Poland, all are sulcate. From Sweden, I have seen 71 females of which 54 or 76% are sulcate; from Finland, 105 females of which 84 or 80% are sulcate; and from Norway, 4 of the 11 or 36% of the females studied are sulcate.

As noted elsewhere (*e.g. D. alaskanus*), the cause of geographic variation in proportion of the two types of females is problematic. The pattern suggests dispersal from particular refugia, but ecophenotypic phenomena cannot be ruled out, nor can a combination of both. The observation that all females of *D. lapponicus lapponicus* are sulcate even though they occupy cold, oligotrophic habitats in the Alps argues against the hypothesis of ecophenotypic expression. Further detailed information of occurrence and relative proportion of both states would be most helpful in attempting an explanation.

Natural history. - What is known of the natural history of this species is summarized fully by F. Balfour-Browne

(1913, 1950:283-284) and Jackson (1956:84-85).

Distribution (map, Fig. 28D). – Very locally distributed in high mountains of southern Europe, with sporadic records for Germany, Switzerland, Holland, Belgium, Scotland and Ireland. Poppius (1910:356) discounts previous records of this species from Iceland.

I have seen the following records which I believe to represent incorrect labelling: "Hongric [?Hongrie], Roussel" (2 CASC, 1 HNHM), Spain (2 ICCM), and Sitka (1 MNHN). There are no recent nor reliable records for North America.

Material examined. – A total of 657 adult specimens were examined, of which 259 were males and 657 were females.

Dytiscus lapponicus disjunctus Camerano 1880, NEW STATUS

Dytiscus lapponicus var. *disjunctus* Camerano 1880:120 (Type locality – Argentara, Piemonte, Italy. Type not seen.). –Zimmermann 1920:249. –Gschwendtner 1923:110. –Guignot 1933:726. –Zimmermann and Gschwendtner 1938:48. –F. Balfour-Browne 1950:280. –Zaitsev 1953:351. –Franciscolo 1979:667.

Derivation of specific epithet. – Presumably, Camerano proposed this name to reflect the isolation of this taxon within the Italian Alps.

Diagnostic combination. – Reduction of pronotal infuscation to a sinuate line acros the pronotal disc and restricted range, in conjunction with the diagnostic combination for the species, are sufficient to identify adult members of *D. lapponicus disjunctus*.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is not shown (see Franciscolo 1979:658, Fig. 2046); coloration of pterothoracic and abdominal sterna in Fig. 12D; median lobe of male not shown; metacoxal processes in Fig. 22J.

Variation. – Shape of pronotal markings of specimens of *D. lapponicus disjunctus* examined is relatively consistent and similar to that illustrated by Franciscolo (1979:658), Fig. 2046).

All of the 38 females seen are sulcate.

If fresh material can be obtained (but see Natural history), it would be useful to determine whether or not flight muscles are present within members of this subspecies. Jackson (1955) suggested that absence of flight muscles from Scottish specimens of the nominate subspecies could have played a role in the limited distribution of that form in Scotland.

Natural history. – Most collection records have no dates associated with them. Available dates are: vii.1898, vii.21, 8.viii.21, viii.23, 22.viii.23. These correlate well with those mentioned by Franciscolo (1979), who further states that he has been unable to collect this subspecies at the type locality despite repeated attempts since 1954.

Intensive collecting by Franciscolo and others has failed to find any other localities for *D. lapponicus disjunctus*. Franciscolo correlates the demise of this taxon with the introduction of trout into the type locality and similar lakes within the Italian Alps. This is very interesting, since F. Balfour-Browne (1913, 1950) mentions that in Scotland *D. lapponicus* is taken only in lochs from which trout are absent. Franciscolo mentions that trout could have preyed upon the immature forms of this subspecies and it may already be extinct.

Distribution (map, Fig. 28D). – All specimens that I have seen were labelled with part of the following compounded label information: Lago della Maddalena, Argenterra, Col de Larche, Valle Sture, Piemonte, Alpi Marittime, 2000 m. Other possible records are treated under Taxonomic notes for *D. lapponicus*.

Material examined. – A total of 50 adult specimens were examined, 12 males and 38 females.

3.27 Dytiscus circumflexus Fabricius, 1801

Dytiscus circumflexus Fabricius 1801:258 (Type area – Tanger *fide* Guignot 1961:860. Type not seen.). –Zimmermann 1920:245. –Müller 1926:299. –Guignot 1933:722. –Houlbert 1934:135. –Zimmermann and Gschwendtner 1938:51. –Guignot 1947a:245. –F. Balfour-Browne 1950:273. –F. Balfour-Browne 1953:27. –Zaitsev 1953:351. –Guignot 1961:860. –Schaeflein 1971:88. –Franciscolo 1979:669.

Dytiscus flavomaculatus Curtis 1825:99 (Type area – not known to me. Type not seen.). –Zimmermann 1920:246.

Dytiscus flavoscutellatus Latreille 1806:331. (Type area – not known to me. Type not seen.). –Zimmermann 1920:246.

Dytiscus excrucians Stephens 1828:503 (Type area – not known to me. Type not seen.). –Zimmermann 1920:246.

Dytiscus dubius Serville 1830:90 *nec* Gyllenhal 1827:373 (Type area – near Paris, France. Type not seen.). –Zimmermann 1920:246.

Dytiscus circumflexus var. *dubius* Serville. –Zimmermann 1920:246. –Müller 1926:299. –Guignot 1933:722. –Houlbert 1934:135. –Guignot 1947a:245. –F. Balfour-Browne 1950:273. –F. Balfour-Browne 1953:27. –Zaitsev 1953:351. Guignot 1961:860. –Schaeflein 1971:88. –Franciscolo 1979:669.

Dytiscus perplexus Boisduval et Lacordaire 1835:302 (Type area – near Paris, France. Type not seen.). –Zimmermann 1920:246.

Dytiscus pisanus var. ♀ *kunstleri* Peytoreau 1894:xlii (Type area – not specifically stated, but probably near Bourdeaux, France. Type not seen.). –Zimmermann 1920:246.

Derivation of specific epithet. – From Latin *circum* meaning "around" and *flexus*, meaning a "bending or turning". The significance of this epithet is unclear to me (perhaps a reference to the frontal chevron).

Notes about type material. – I have not seen the types of any of the various names applied to this species. Therefore, assignment of the names follows traditional useage (*e.g.* Zimmermann 1920). Explanation of Peytoreau's var. *kunstleri* is required. Most Palearctic workers such as Zimmermann have treated this name as if it were assigned species level status. This may be because these authors had not seen the original description published in a little known journal that is difficult to obtain. After reading the original description, I was unsure whether Peytoreau had described a specimen of *D. pisanus* or *D. circumflexus*. Reference to Peytoreau's figure of metacoxal processes definitely indicates the latter, as the processes are much too aciculate for members of the former.

Diagnostic combination. – All but four of the specimens examined have maculate abdominal sterna. This, in combination with acuminate metacoxal processes and principally European and North African distribution, should allow easy separation of most specimens. For problematic specimens, reference to features of the median lobe of males is essential, and females are best determined by association with males from the same region.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5D; coloration of pterothoracic and abdominal sterna in Fig. 13A; median lobe of male in Fig. 20A; and metacoxal processes in Fig. 22K.

Taxonomic notes. – This species is the most varied in body shape, yet the form of the apex of the median lobe is quite constant. Far eastern Palearctic records of this species probably result from confusion with *D. sinensis*, which is quite similar in markings of the venter.

The species *D. circumflexus*, *D. thianshanicus*, *D. latro* and *D. sinesis* comprise a monophyletic group of some complexity. As presently interpreted, they form a geographical replacement series extending through the Palearctic Region, basically from west to east, the taxa in the sequence indicated above. Of these four species, *D. circumflexus* (except as noted under variation) and *D. sinensis* are similar in ventral colour pattern (*i.e.* pterothoracic and abdominal sterna fasciate), while specimens of *D. thianshanicus* and *D. latro* have most of the venter yellow. The best characters for their separation are details of the form of the median lobe of males. Scanning electron micrographs of the apical portions of the median lobe of male specimens are presented in Figs. 20A-D. Taxonomically important character states of the median lobe for each species are as follows: 1) shape of posterior protion of knob in ventral view – notched (*D. circumflexus*), triangularly extended posteriorly and fading into the ventral ridge (*D. thianshanicus* and *D. sinesis*), or evenly truncate (*D. latro*); 2) width of apical knob relative to that of preapical portion – knob much narrower than preapical protion (*D. circumflexus* and *D. thianshanicus*), and knob somewhat narrower than preapical portion (*D. latro* and *D. sinensis*); 3) prominence of apical knob in lateral view – not very prominent (*D. circumflexus*, *D. thianshanicus* and *D. latro*), and very prominent or spatulate (*D. sinensis*); 4) widening of ventral ridge in ventral view – abruptly (*D. circumflexus*) or evenly tapered (*D. thianshanicus*, *D. latro* and *D. sinensis*); 5) in lateral view, the relative width of dorsal and ventral portions of median lobe just anterior to its greatest width (using lateral ridge and a dividing line) – dorsal portion much narrower than ventral portion (*D. circumflexus* and *D. thianshanicus*), dorsal and ventral portions approximately equal (*D. latro*), and dorsal much wider than ventral portion (*D. sinensis*).

Variation. – Specimens of this species exhibit a great deal of variation in body shape or habitus. This may be part of the reason for proposal of many of the names listed above. For instance, most male specimens have pronota wider than elytra and most females have pronota equal or subequal to elytra at the base. However, some males have pronota only as with as that of most females, and some females have very narrow pronota so that the pronotal-elytral juncture appears emarginate. Such differences in pronotal shape drastically alter overall appearance of specimens. These characters are consistent within many local populations, but population samples from surrounding areas may show opposite extremes.

Most specimens have the venter marked with black (Fig. 13a left). However a few specimens have a completely yellow venter (*e.g.* from Sweden (Skåne), Czeckoslovakia (Moravia), Hungary (Kolocsa), and Iran). There is little geographic correlation to this pattern except that the atypical specimens occur along the eastern edge of the range, although specimens with a typical pattern are found at the western-most locality in Afghanistan.

In Europe, excluding Great Britain, most female specimens are not sulcate. Scattered records of sulcate females are available for Sweden, France, Holland, Germany, Prussia or Poland, Corsica and Crete, as well as the Ahaggar Mountains of Algeria. In Great Britain, F. Balfour-Browne (1950:274) states that sulcate females predominate. Thus the trend is for more northern samples to be sulcate, whereas more southern samples are predominantly non-sulcate, and the most southern (but montane) samples are also sulcate.

Natural history. – A summary of the natural history of this species is presented by F. Balfour-Browne

(1950:272-277).

Distribution (map, Fig. 29A). – All specimens of *D. circumflexus* that I have seen are from Europe, northern Africa and Asia Minor. More eastern records (*e.g.* Siberia, by Zaitsev 1953:329) probably refer to *D. latro* and records for Kazakhstan (*e.g.* Konev 1976) need to be re-examined in light of the previously inadequately understood *D. thianshanicus*. Records of *D. circumflexus* for the Canary Islands (F. Balfour-Browne 1950:276) need to be confirmed.

Chorological relationships. – Until the eastward extension of the range of *D. circumflexus* is better defined, it is difficult to list the taxa with which this species is sympatric. Within Europe, it is sympatric with *D. semisulcatus*, *D. mutinensis*, *D. dimidiatus*, *D. pisanus*, *D. marginalis*, *D. latissimus*, *D. circumcinctus* and *D. lapponicus*. It may be sympatric with *D. persicus* in Iran, but more records are needed to establish this with certainty.

Phylogenetic relationships. – *D. circumflexus* (if its distribution pattern is confirmed as suggested above), *D. thianshanicus* (south-central U.S.S.R.), *D. latro* (Siberia) and *D. sinensis* (northern China) seem to form a stepwise pattern suggesting vicariance and/or ecological replacement. This is supported by phylogenetic analysis (Fig. 30). These four taxa are united by common possession of a well-developed constriction of the apex of the median lobe just before the apical knob (Figs. 20A-D, dorsal view), and share with their sister group (*D. lapponicus*) very elongate metacoxal processes.

Material examined. - A total of 546 adult specimens of *D. circumflexus* were seen. Of these, 216 were males and 229 were females. Sex was not determined for one specimen.

3.28 **Dytiscus thianshanicus** Gschwendtner, 1923

Dytiscus thianshanicus Gschwendtner 1923:107 (Type locality – "Aksu-Tal am Südabhang des Thian-schan" = Jachsu River Valley, Kuljab district of Tadžik S.S.R. Type not seen.). –Zimmermann and Gschwendtner 1938:53. –Zaitsev 1953:352.

Derivation of specific epithet. – Derived from the name of the mountain range in which the type locality is found.

Diagnostic combination. – A combination of south-central Palearctic distribution, predominantly yellow venter, spinose metacoxal processes, lack of narrow yellow ring around eye, and distinctive form of apex of median lobe of males adequately distinguish members of this species.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5E; coloration of pterothoracic and abdominal sterna in Fig. 13B; median lobe of male in Fig. 20B; and metacoxal processes in Fig. 22L.

Taxonomic notes. – This species is still inadequately known. Members of *D. thianshanicus* are difficult to separate from those of *D. latro* except on the basis of form of the apex of the median lobe and distribution. The latter feature is of doubtful value, for ranges of both taxa are inadequately known. See also taxonomic notes under *D. circumcinctus*.

Variation. – Too few specimens were seen to establish whether or not there are geographic patterns of variation. No sulcate females were seen but this may be due to the small number of specimens studied.

Natural history. – I can find nothing published about natural history of this species, nor does the scanty label data supply any information.

Distribution (map, Fig. 29B). – I have seen specimens only from south-central U.S.S.R.

Chorological relationships. – This species is known to be sympatric (but see above) with *D. marginalis marginalis*, *D. circumcinctus* and *D. latissimus*. It may also be sympatric with *D. semisulcatus*, *D. persicus* and *D. dauricus*.

Phylogenetic relationships. – See similar section in treatment of *D. latro*.

Material examined. – A total of 10 specimens of *D. thianshanicus* were examined and of these 6 were males and 4 were females.

3.29 Dytiscus latro Sharp, 1882

Dytiscus latro Sharp 1882:644 (Type locality - "Mantchuria". Holotype non-sulcate female in BMNH labelled as follows: Type [circular orange-rimmed label]; Manchuria; Sharp Coll. 1905-313 [label inverted]; Dytiscus latro, Sharp type; Mantchuria Mus. Castelnau 948; HOLOTYPE, Dytiscus latro Sharp, examined R.E. Roughley 1981.). —Zimmermann 1920:249. —Zimmermann and Gschwendtner 1938:53. —J. Balfour-Browne 1946:453. —Zaitsev 1953:353.

Dytiscus piceatus Sharp 1882:644 (Type locality - "Eastern Siberia; (Irkutsk)". NEW SYNONYMY. Holotype male in BMNH labelled as follows: Type [circular orange-rimmed label]; Irkutsk, Siberia; Sharp Coll. 1905-313 [label inverted]; Dytiscus piceatus, Sharp type; Irkutsk, Siberia, 949; HOLOTYPE, Dytiscus piceatus Sharp, examined R.E. Roughley 1981). —Zimmermann 1920:253. —Zimmermann and Gschwendtner 1938:52.

Dytiscus stadleri Gschwendtner 1922:93 (Type locality - "Berisovka, Transbaikalien". Holotype male in ZSBS labelled as follows: "Type; [illegible handwriting, perhaps = Berisovka]; HOLOTYPE, Dytiscus stadleri Gschwendtner). —Zimmermann and Gschwendtner 1938:53. —J. Balfour-Browne 1947:453.

Derivation of specific epithet. - Latin *latro* means hireling, robber or brigand. The significance is not known.

Diagnostic combination. - A combination of eastern Palearctic distribution, predominantly yellow venter, spinose metacoxal processes, lack of narrow yellow ring around eye and distinctive form of apex of median lobe of males should adequately distinguish members of this species.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 6A; coloration of paterothoracic and abdominal sterna in Fig. 13C; median lobe of male in Fig. 20C; and metacoxal processes in Fig. 22M.

Taxonomic notes. – The taxonomic problems associated with *D. latro* are a result of inadequate description (and therefore poor dissemination of Sharp's concept), association of sexes, and too few available specimens. The latter feature remains the most critical. Sharp may have suspected that *D. latro* and *D. piceatus* were representative of the same taxon, but does not clearly state this. Gschwendtner would have had difficulty assigning his specimen to *D. latro* based on the original description, and therefore described *D. stadleri*. Either he or Zimmermann noticed the error and provided the synonymy, although this is not clearly indicated in their publication, nor are their reasons for synonomizing them.

Sharp discussed both *D. latro* and *D. piceatus* on the same page of his monograph but *latro* occurs first, and is thus the valid name for this taxon.

Based primarily on the form of the median lobe of the male, this species appears distinct. Assignment of females is more difficult because of their similarity to females of *D. thianshanicus*. The most reliable means I have found is association with males and distributional differences. More specimens need to be examined before the present arrangement is treated as more than provisional.

Variation. – Too few specimens were seen to establish whether or not there are geographic patterns of variation. No sulcate females were seen, but this may be due to the small number of specimens seen.

Natural history. – I can find nothing published on the natural history of this species, nor does the scanty label data supply any information.

Chorological relationships. – The entire range of this exclusively east Palearctic species is insufficiently known. However, it is known or inferred to be sympatric with *D. sharpi*, *D. marginalis czerskii*, *D. delictus*, *D. circumcinctus*, *D. lapponicus lapponicus* and *D. latissimus*. Establishment of the western limits of *D. latro* and the eastern limits of *D. thianshanicus* would be helpful in determining the taxonomic status of these two taxa.

Phylogenetic relationships. – The sinuate lateral margins and well developed sensory pores on the knob of the median lobe of males, and spinose metacoxal processes indicate close relationship to *D. lapponicus*, *D. circumflexus*, *D. thianshanicus*, and *D. sinensis*. In Fig. 30, I have interpretted *D. latro* as the eastern vicar of the central Palearctic *D. thianshanicus*.

Distribution (map, Fig. 29C). – This taxon occurs in the eastern U.S.S.R. (described loosely as Siberia) and adjacent Manchuria.

Material examined. – A total of 17 specimens were examined, of which four are males and 13 females.

3.30 Dytiscus sinensis Feng, 1935

Dytiscus sinensis Feng 1935:182 (Type locality – Yin-Kuan-Tsai, Szechuen, China. Holotype male in USNM labelled as follows: Szechuen, CHINA, DCGraham; Yin-Kuan-Tsai, 12300 ft, vii.21.30; Dytiscus sinensis (Type) H.T. Feng). –Feng 1937:14. –Zimmermann and Gschwendtner 1938:27.

Derivation of specific epithet. – The specific epithet means Chinese.

Diagnostic combination. – A combination of eastern Palearctic distribution, fasciate abdomianl sterna, spinose metacoxal processes, and spatulate form of apex of median lobe of males (in side view) adequately distinguish members of this species.

Description. – Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 6B; coloration of pterothoracic and abdominal sterna in Fig. 13D; median lobe of male in Fig. 20D; and metacoxal processes in Fig. 22N.

Taxonomic notes. – This species appears to be quite distinctive despite the few specimens seen by both Feng and me.

Variation. – Too few specimens were seen to establish whether or not there are geographic patterns of variation. No sulcate females were seen but this may be due to the small number of specimens seen.

Natural history. — I can find nothing published on the natural history of this species, nor does the scanty label data supply any information.

Distribution (map, Fig. 29D). — I have seen specimens from the type locality only. Feng adds Shensi (=Shanxi Province, China) and Manchuria.

Chorological relationships. — Generalizing from the distribution, this species may be sympatric with *D. marginalis czerskii*, *D. delicutus*, *D. circumcinctus*, *D. lapponicus*, *D. latro* and possibly *D. latissimus*. The altitude given for the type specimen may indicate an affinity for high altitude habitats, reducing co-occurrence with other species.

Phylogenetic relationships. — The *D. dauricus*-group falls into two subgroups. *D. sinenis* is in the more apotypic of these groups (characterized by the character states discussed under *D. latro*), and within this subgroup shows the highest number of apotypic features.

Material examined. — A total of 10 specimens of *D. sinensis* were examined, all from the type locality. Three are males and seven are females.

4. Phylogeny and Zoogeography of Dytiscini

4.1 Introduction

In this section, I present reasons for regarding the tribe Dytiscini and genus *Dytiscus* as monophyletic. Then, I deal in some detail with the evolution of *Dytiscus*, from holomorphological, ecological and chorological points of view.

Methods used for reconstruction of the phylogeny of members of *Dytiscus* are discussed in Ball and Roughley (1982), Roughley and Pengelly (1982) and references cited therein. Also, see the excellent treatment by Ashe (1982:225-229). Characters and character state distribution by taxon are shown in Table 3. The reconstructed phylogeny is shown in Fig. 30. Character state polarity was deduced from *ex*-group occurrence in members of Dytiscinae. The most easily resolved character consists of two character states found in two groups of taxa. For example, members of Dytiscinae, exclusive of *Dytiscus*, possess rounded metacoxal lobes, whereas members of *Dytiscus* possess either rounded or variously elongated or pointed metacoxal lobes. The unique state expressed only by some members of *Dytiscus* is therefore considered apotypic for them (Watrous and Wheeler 1981).

Many character states are not discretely distributed, however. Various states of a character can evolve independently by reversal, parallelism, or even convergence (see discussion in Gauld and Mound 1982, and Wiley 1981:12-13, 120-122). Some features of subsets of *Dytiscus* (species-groups, sets of species-groups) were polarized and homoplasies established by means of the *in*-group criteria discussed by de Jong (1980) and Watrous and Wheeler (1981). Most examples of characters of equivocal polarity could be analyzed because of their co-occurrence with more easily established (heavily weighted) character trends (de Jong 1980).

4.2 Holomorphological aspects: Dytiscini and Dytiscus

4.2.1 Dytiscini as a monophyletic unit

The tribe Dytiscini is comprised of two genera, the dibasic Australian and Tasmanian *Hyderodes* Hope (Watts 1978), and the more diverse Holarctic *Dytiscus*. Sharp (1882:939) was not convinced of the naturalness of this tribe: "...the resemblance or approximation between Dytiscus and Hyderodes does not arise from genetic connection (or common origin), but is due to a parallelism in the environment of the organisms during their evolution." Sharp does not mention what these environmental similarities might be.

I disagree with Sharp's hypothesis. This is in part based upon the characters which Sharp himself has provided

(1882:937-939). The first of two characters, which I interpret as synapotypic for Dytiscini, is size. The total range of size within the tribe is from 19 to 44 mm, and is not approached by many groups of Hydradephaga except Cybistrini, which range from 13 mm (Brinck 1945) to 47.5 mm (Sharp 1882:713). Large size has evolved independently in members of Dytiscini and Cybistrini.

Sharp (1882:240, 938) discusses the much enlarged spiracular openings of the last two abdominal terga, which are unique to Dytiscini. This character state, then, is also a synapomorphy for the members of the tribe.

4.2.2 Dytiscus as a monophyletic unit

At least five characters indicate the monophyly of *Dytiscus*. Some of these are difficult to polarize, but in totality they probably indicate the phylogenetic uniqueness of this genus.

1) Large size. Specimens of *Dytiscus* range from 22.6 to 40.0 mm (Table 2) in length, and most are in the range 24 to 30 mm. Specimens of *Hyderodes* are 19 to 20 mm in length (Sharp 1882:633, 644 and Watts 1978:138; Note: the length of 10.9 mm given by Watts for specimens of *H. crassus* Sharp must be a misprint).

2) Clypeal-frontal suture entire (epistomal sulcus). Sharp (1882:904) mentions that the clypeal suture is complete and distinct throughout its entire length. This is unique among members of the family Dytiscidae, and represents a

state similar to that of at least Hygrobiidae, Amphizoidae Trachypachidae and Carabidae. Its presence in specimens of *Dytiscus* is interpreted as re-acquisition of this character.

3) Male mesotarsus with very numerous palettes. Male specimens of *Dytiscus* have more than 700 to 1000 palettes per mesotarsal acetabulum. This state is not approached by any other member of Dytiscinae that I have examined. For instance, specimens of *Hyderodes* have 18 palettes per mesotarsal acetabulum. Nevertheless, this character is difficult to polarize. It is unique within Dytiscinae, but is similar to the state found in many members of Colymbetinae. Relatively numerous palettes probably represent a plesiotypic state (*e.g.* see discussion in Roughley and Pengelly 1982 for Hydaticini) in certain groups of Dytiscidae, but rarely, if ever, does it approach the numerical abundance found in males of *Dytiscus*. Therefore, I interpret the condition found in this genus as apotypic.

4) Very large spiracular stigma of two apical abdominal terga. Members of Dytiscini are characterized by large stigmata (see above), which in *Dytiscus* are much larger than those of *Hyderodes*.

5) Triangular shape, in cross-section, of apical portion of median lobe. In the discussion of character 7.3 used in the phylogenetic analysis, I characterize the plesiotypic form of the median lobe of male Dytiscinae. Male specimens of *Hyderodes* closely resemble this generalized form. In particular, the apical portion (posterior to

flanges) is blade-like, and therefore oval in cross-section. Male specimens of *Dytiscus*, in contrast, have the median lobe more or less widened laterally, and thereby present a triangular cross section of the apical portion.

4.3 Evolution of Dytiscus: holomorphological aspects

4.3.1 Characters used in phylogenetic analysis

In this section, I list each character in the order in which it appears on Fig. 30, although the reference to the characters by numerals is as in Table 3. States of each character are listed along with the suggested transformation series they form, and the basis for this polarity.

Character A. Segmentation of labial palpomere I of third-stage larva. Two states: plesiotypic, one-segmented; apotypic, two-segmented. Basis for classification: *ex*-group.

Character 3.1. Explanation of pronotum. Two states: plesiotypic, explanate; apotypic, not explanate. Basis for classification: *in*-group.

Character 5.1. Elytron of female. Two states: plesiotypic, not sulcate, and therefore male-like; apotypic, sulcate. Basis for classification: *ex*-group.

Character 7.1. Lateral ridges of median lobe. Two states: plesiotypic, present; apotypic, absent. Basis for classification: *ex*-group

Character 6.1. Distribution of palettes on male mesotarsal acetabulum. Two states: plesiotypic, evenly distributed; apotypic, with glabrous area centrally. Basis for classification: *ex*-group.

Character 7.5. Relative length of dorsal and lateral flanges of median lobe of male. Two states: plesiotypic, dorsal equal to, or longer than laterals; apotypic, dorsal much longer than laterals. Basis for classification: *ex*-group and *in*-group.

Character 4.6. Shape of apex of metacoxal process. Four states: plesiotypic, rounded; first apotypic, acute; second apotypic, acuminate; third apotypic, acuminate and elongated. Basis for classification: *ex*-group and *in*-group.

Character 4.7. Shape of inner margin of metacoxal process. Two states: plesiotypic, convex; apotypic, concave. Basis for classification: *ex*-group.

Character 7.3. Curvature of pre-apical portion of median lobe of male. Two states: plesiotypic, linear; apotypic, curved. Basis for classification: *ex*-group.

Characters 4.1 - 4.5. Colour of pterothoracic sterna. Three states: plesiotypic, black; first apotypic, black and yellow (fasciate); second apotypic, yellow. Basis for classification: *ex*-group and *in*-group.

Character 7.6. Roundedness of tip of median lobe of male. Three states: plesiotypic, not rounded; first apotypic, rounded; second apotypic, broadly rounded. Basis for classification: *ex*-group.

Character 7.7. Development of tip of median lobe of male. Two states: plesiotypic, without knob; apotypic, knobbed. Basis for classification: *ex*-group.

Character 7.9. Extension of pre-knob portion of median lobe of male. Two states: plesiotypic, not extended; apotypic, extended. Basis for classification: *in*-group.

Character 7.8. Development of sensory-type pores on tip of median lobe of male. Two states: plesiotypic, absent or, if present, small; apotypic, distinct. Basis for classification: *ex*-group and *in*-group.

Character 7.2. Curvature of apex of median lobe of male (lateral view). Two states: plesiotypic, straight; apotypic, curved. Basis for classification: *ex*-group and *in*-group.

Character 7.4. Profile of pre-apical portion of median lobe of male (dorsal view). Two states: plesiotypic, parallel-sided; apotypic, sinuate. Basis for classification: *ex*-group and *in*-group.

Character 7.10. Relative development of knob of median lobe of male. Two states: plesiotypic, moderate; apotypic, significant. Basis for classification: *in*-group.

Character 7.11. Profile of pre-apical portion of median lobe (dorsal view). Two states: plesiotypic, wider or more robust; apotypic, thinner or less robust. Basis for classification: *in*-group.

4.3.2 Discussion of characters and homoplasy

My interpretation of some characters is not completely apparent from simple description of the characters and their states. The following section explains more fully some characters and justifies my interpretation of others.

Character A. Segmentation of labial palpomere I of third-stage larva.

Blunck and Klynstra (1923) discuss the secondary or superimposed segmentation of head appendages of larval stages of species of *Dytiscus*. In the discussion of phylogenetic relationships of *D. verticalis*, the one-segmented labial palpomere I of larvae (Wilson 1923, Fig. 37), was noted to be similar to that of members of *Hyderodes shuckardi* (Watts 1964, Fig. 37). Subsequent study has confirmed the lack of false segmentation of this palpomere in larvae of both of these species.

I have associated adult and third-stage larvae of all Nearctic species except *D. hatchi* (Roughley, unpublished data), and the larvae of European species of *Dytiscus* were described by Blunck and Klynstra (1923). Therefore, while known distribution of this character is incomplete (larvae of some eastern Palearctic species of *Dytiscus* are unknown), it is sufficient to suggest its use as a synapomorphy for all species of *Dytiscus* other than *D. verticalis*.

Character 3.1. Explanation of pronotum.

Laterally explanate pronota are unique to adult

Dytiscus among Dytiscinae. As such, this character state is synapotypic for members of *Dytiscus*, though secondarily absent from members of the *D. hybridus*-group.

This character is sexually dimorphic in adults of *D. cordieri* (pronotum explanate in females, only). I deem absence of the explanation in males as a loss of the apotypic condition, and thus an evolutionary reversal.

An alternate phylogeny suggested by the distribution of this character would be one in which the *D. verticalis*- and *D. hybridus*-groups were interchanged in Figure 30. This would result in explanate pronota representing a synapotypy for all species-groups of *Dytiscus* except the *D. hybridus*-group, rather than for *Dytiscus* as a whole. Also, the derived state of Character A would be unique to a single monobasic species-group (*D. verticalis*). There is little corroborating evidence for either of these hypotheses. I have chosen the representation shown in Figure 30 because specimens of *D. verticalis* exhibit less derived character states than do members of the *D. hybridus*-group, and is thus closer to the hypothetical ancestor of the genus

Character 6.1. Distribution of palettes on male mesotarsal acetabulum.

In all adult male dytiscines examined, palettes of the mesotarsus are more or less evenly distributed. In specimens of *D. hybridus* and *D. marginicollis*, the acetabulum has a central, longitudinal glabrous area. This is considered an apotypic state. Given that these two members of the

D. hybridus-group are the only extant species of *Dytiscus* which have such glabrous areas, and that it is achieved in a similar manner, suggests that, even though it is a loss, it is a structural synapotypy for these two taxa. As mentioned under the phylogenetic treatment of *D. hybridus*, this species represents my concept of the hypothetical ancestor of the group, except that it would have had evenly distributed tarsal palettes.

In the absence of this character, I would have rearranged the *D. hybridus*-group, placing *D. hybridus* as the sister group to a lineage including *D. harrisii*, *D. marginicollis* and *D. habilis*. This would have allowed simpler explanation of characters 3.2, 4.2-4.5, 7.1 and 7.5 (see Table 3). The first five of these characters are colour-related, and markedly variable (see Table 7 for Character 4.5"). Character 7.2 is discussed elsewhere in this section as being of low phylogenetic weight, and character 7.5 would still require one within-species-group reversal for the state found in males of *D. habilis*. The question is whether or not seven synapotypies of low weight are more significant than one of higher weight. My interpretation demands a negative answer to this question, or demonstration of a single character better than distribution of tarsal palettes. In the absence of the latter, I retain the arrangement shown in Figure 30.

Character 7.5. Relative length of dorsal and lateral flanges of median lobe.

Dorsal and lateral flanges of the median lobe are used as guides for the spermatophore during its transfer to, and depostion in, the female's bursa copulatrix (Demandt 1924). In most species of *Dytiscus*, and in species of *Hyderodes*, the two sets of flanges are subequal in length. In some members of both the *D. hybridus*- and *D. semisulcatus*-groups, there is a marked discrepancy in length, presumably brought about by a decrease in length of the lateral flanges. On Figure 30, I have used the apotypic state (dorsal flange longer than lateral flanges) to isolate the *D. semisulcatus*-group. This requires that the apotypic state be derived three times: once in *D. hybridus*, once in *D. habilis*, and once in the common ancestor of the *D. semiculcatus*-group. Furthermore, there is a reversal from the apotypic to the plesiotypic state in one member of the *D. semisulcatus*-group (*D. sharpi*). The alternate arrangement of grouping all species which possess the apotypic state (*D. hybridus*, *D. habilis*, *D. semisulcatus*, *D. carolinus*, *D. fasciventris*, and *D. hatchi*) seems unlikely, because it would mean that sulcate elytra had evolved more than one time (Character 3.1).

Characters 4.6 and 4.7. Shape of metacoxal processes.

The most common form of metacoxal process of members of Dytiscinae is a rounded metacoxal lobe (*i.e.* not angulate), with inner margin convex. Increasing angle of apex of the metacoxal process is a heavily weighted character within my phylogenetic analysis. The three apotypic states represent a transition series easily polarized by comparison to specimens of *Hyderodes* and other Dytiscinae. The second apotypic state is coincident with concave inner margin of the metacoxal process. They are perhaps separate characters, because there is no intermediate character state for shape of the inner margin of the metacoxal process.

Heavy weighting of this character forces recognition of homoplasies in other characters. For example, presence of a knob at the apex of the median lobe of males (Character 7.7) isolates members of the *D. marginalis*- and *D. dauricus*-groups, except for *D. latissimus* and *D. alaskanus* of the latter group. A lesser weight placed on Characters 4.6 and 4.7 would allow these two species to be placed in a separate group as a sister lineage to the remainder of the *D. marginalis*- plus *D. dauricus*-groups. This arrangement would suggest that acuminate metacoxal processes with a concave inner margin evolved more than once.

I have chosen to retain Characters 4.6 and 4.7 as heavily weighted because they form a clear morphocline which is easily polarized, and because other arrangements would precipitate recognition of many more homoplasies. For example, the re-arranged phylogeny suggested above would bring about two (as opposed to one) independent developments of the apotypic state of Character 7.8, four (as opposed to three) of Character 7.2, and two each (opposed to one each) of Characters 4.6 and 4.7, discussed above.

Character 7.3. Curvature of preapical portion of median lobe of male.

Roughley and Pengelly (1982:280) characterized the plesiotypic hydaticine median lobe as parallel-sided, with unmodified tip. These characters in conjunction with a generally blade-like form of the median lobe comprise the ancestral form of the median lobe of males of Dytiscinae.

Within *Dytiscus*, the apotypic state has evolved at least three times: in *D. hybridus*-group (*D. marginicollis*), in *D. semisulcatus*-group, and is also found in the more advanced species-groups, but lost in *D. pisanus*. The sporadic parallelisms and the reversal of the apotypic state of this character are perhaps not surprising when it is considered that the change is simple and probably easily achieved in the evolution of various lineages. It is therefore to be considered a character of low importance for reconstruction of a phylogeny.

Characters 4.1 - 4.5. Colour of pterothoracic sterna.

Ventral coloration among species of *Dytiscus* is variable within species as well as within species-groups, and both apotypic states have occurred independently in a number of lineages. Among members of *Dytiscus*, however, there is a generalized group trend from darker to lighter in all colour-related characters (2.1, 3.2, 3.3, 4.1-4.5: see Table 3). All are characters of low phylogenetic weight.

Character 7.7. Development of tip of median lobe of male.

The generalized *ex*group form of the median lobe of dytiscines is discussed under the treatment of Character 7.3. The derived state of this character unites the *D. marginalis*- and *D. dauricus*-groups. Within the latter, absence of the apotypic state from male specimens of *D. latissimus* and *D. alaskanus* represent secondary, independent losses, as discussed under Characters 4.6 and 4.7 above.

Character 7.9. Extension of pre-knob portion of median lobe of male.

The apotypic condition as represented by members of the *D. marginalis*-group consists of a narrowing and elongation of the pre-apical portion just before the apical knob. The apotypic condition of this character is distinct from that of Character 7.11, discussed below, in which the entire pre-apical portion is narrowed.

Character 7.2. Curvature of apex of median lobe of male (lateral view).

The primitive form of the median lobe is discussed under the treatment of Character 7.3. Subsequent modification of this basic plan has occurred many times in the history of the subfamily (group trend, *e.g.* see Roughley and Pengelly 1982). Within *Dytiscus*, there is evidence of the plesiotypic state of this character in the plesiotypic members of two lineages (*D. verticalis* and *D. harrisii*) and of three independent derivations of the apotypic state (*D. sharpi*, *D. pisanus*, and all but two members of the *D. dauricus*-group). This character is similar to Character 7.3 in that conversion to the apotypic state is probably easily accomplished and is thus considered to be of low phylogenetic weight.

Character 7.10. Relative development of knob of median lobe of male (dorsal view).

The apotypic state of this character is relative and subjective. However, the distinctiveness of the change is apparent. The apotypic state of this character would be coincident with that of Character 7.11 if it were not for *D. circumflexus*, males of which have a very distinctive apical knob, but the apex is not excessively narrowed.

4.3.3 Evolution of genitalia of males of Dytiscus

I have assigned form of the median lobe of male genitalia some importance for both recognition of species level status and for phylogenetic analysis. The male genitalia are much more than simply a set of characters, and must be treated as a functional evolutionary unit. Therefore, the purpose of this section is to trace the history of the male genitalia as detailed by the reconstructed phylogeny proposed (Figure 30). My method has involved description of a hypothetical type of genitalia, to which are assigned the characteristics I believe to be primitive, and then to discuss the form and modification of the median lobe from primitive through derived species-groups.

Ancestral dytiscines probably possessed a J-shaped median lobe with the longer portion, or shaft, parallel-sided, with an unmodified, straight, blade-like tip (based in part on Roughley and Pengelly 1982:280). Located dorsally on the median lobe are two lateral and one dorsal flange, which form a guide, or channel, for the spermatophore during copulation (Demandt 1924). This form of median lobe, except for the straight tip, is seen in extant *Prodaticus*, a basal hydaticine, and *Hyderodes*, a basal dytiscine.

Coincident with origin of the genus *Dytiscus* was derivation of a median lobe with a triangular cross section (see Point 5 in Section 4.2.2). The plesiotypic, blade-like condition was modified by lateral extension of the sides and perhaps also by a strengthening of the ventral ridge. These steps have created the triangular form of the apex. The form of the median lobe closest to this ancestral type within *Dytiscus* is seen in specimens of *D. verticalis* (Fig. 14A), and *D. harrisii* (Fig. 14B).

Earlier, I discussed the form of the apex of the median lobe as the major taxonomic criterion for delimiting species level taxa, and noted the uniformity of this character within species. This implies that there is selection for uniformity within species, and that difference in form of the apex of the median lobe could be an isolating mechanism for species. This latter point is exemplified by members of the *D. hybridus*-group (Figs. 14B-D, 15A). As mentioned above, *D. harrisii* has the plesiotypic form within the group. The median lobe of *D. marginicollis* is similar to that of *D. harrisii* except that the tip is abruptly deflexed. The widely allopatric *D. hybridus* and *D. habilis* have shortened lateral flanges, lack distinct lateral ridges, and have slightly (*D. hybridus*) or more prominently (*D. habilis*) modified tips. In addition, the pre-apical portion of the median lobe of *D. hybridus* is slender, whereas it is greatly thickened in male *D. habilis*. In summary, modification of five characteristics within three species has produced four radically different forms of the median lobe.

Within the *D. semisulcatus*-group (Figs. 15B-D, 16A-B), the nominate species has the median lobe similar to that of the plesiotypic form but less triangular and with the dorsal flange greatly elongated. An elongated dorsal flange is found in three other species of the group (*D. sharpi* is the exception). All but the nominate species have the tip abruptly deflexed, although it is more deflexed in *D. sharpi* than in the others, and males of this taxon also have the tip modified. The median lobe of *D. carolinus* and *D. hatchi* lack any remnant of a lateral ridge, whereas that of *D. fasciventris* exhibits it, although only apically. Conversely, the median lobe of males of *D. carolinus* and *D. fasciventris* share a curious subapical depression when seen in dorsal view.

It is interesting that the members of this group are largely allopatric and yet show a high degree of divergence in the form of the median lobe and that the three Nearctic species have the most similar form of the median lobe. The former is probably due to the long isolation of the species of this group, and the latter to more recent speciation among them than between them and the other members of the clade. Members of this group exhibit modifications in the same five characteristics found in the *D. hybridus*-group, but show more stages of some of these (*i.e.* deflection of the tip, reduction of lateral flanges, and effacement of lateral ridge) and added another characteristic (dorsal depression).

The *D. dimidiatus*-group is characterized by a rounded tip of the median lobe (Figs. 16C-D, 17A-B). All have the apex deflexed, and all but the Nearctic *D. cordieri* have the tip quite broadly rounded, with distinct lateral ridges. Specimens of *D. cordieri* exhibit some characters of the plesiotypic form except those noted above, and the swollen area above the place the lateral ridges would normally be located. Specimens of the Palearctic species *D. mutinensis* and *D. dimidiatus* are very similar in form and, as argued in the text, this is perhaps best considered as an example of recent speciation. Co-occurring geographically with these latter two species is *D. pisanus* of which the apical portion of the median lobe has a host of unique characteristics, such as very broad tip, sinuate lateral margin (in lateral view), and great development of ventral setation towards the apex. Members of the *D. dimidiatus*-group thus show, in form of, and subsequent modification of the median lobe, few similarities to the previously discussed species-groups of *Dytiscus*.

Both the *D. marginalis*- and *D. dauricus*-groups are characterized by presence of a distinct knob on the median lobe (secondarily lost by members of *D. alaskanus* and *D. latissimus* of the latter species-group). The *D. marginalis*-group (Figs. 17C-D, 18A-B) is unique because of the extension of the pre-apical knob portion (Character 7.9). All species have subequal flanges, distinct lateral ridges, and a general similarity in form. There are minor differences in shape of the knob when seen in ventral view, and the relative thickening of the ventral ridge. All of the four forms included in this group occur exclusively in the Palearctic region. Of these only *D. marginalis czerskii* and *D. delictus* are broadly sympatric. In the latter, the apex of the median lobe is stouter and the distance from the tip to the dorsal flange is appreciably shorter. Therefore, in this group of species, the integrity of taxa is perhaps more sustained by allopatry and other differences in life history than by divergence in form of the median lobe.

As mentioned previously, two members of the *D. dauricus*-group (Figs. 18C-D, 19,20) have lost the apical knob of the median lobe, yet the median lobe of both species remains qualitatively different. All species have deflexed apices, distinct lateral ridges and subequal dorsal flanges. The apical portion of the median lobe is flatly arched in *D. circumcinctus* (using the lateral ridge as a reference point), and more abruptly arched in more advanced species (except *D. alaskanus*), which also have sinuate lateral margins (in dorsal view). Members of *D. circumcinctus* and all other advanced species have well-developed sensory-type pores on the apical knob. Their function is unknown to me. Specimens of *D. circumcinctus*, *D. thianshanicus*, *D. latro* and *D. sinensis* all possess a quite prominent knob at the apex, and the latter three taxa have a distinctly thinner pre-apical portion (in dorsal view) which produces an even greater prominence of the apical knob.

As in the *D. marginalis*-group, the degree of differentiation between species based on the form of the apex of the median lobe is less dramatic within the *D. dauricus*-group than in the *D. hybridus*- and *D. semisulcatus*-groups. However, within the *D. dauricus*-group, unlike the *D. marginalis*-group, many species of the former occur sympatrically. This could be interpreted as reflecting less reliance on the median lobe as an isolating mechanism, although the fact that each form of apex is distinctive somewhat negates this. It seems more reasonable to suggest that at least some members of the *D. dauricus*-group have arisen more recently than have species of some other groups, and therefore have had less available time for divergence. Other isolating factors associated with life history could be operating to augment the mechanical isolation supplied by genital differences.

Of the six species-groups recognized within *Dytiscus*, members of two (*D. verticalis*- and *D. hybridus*-groups) have a median lobe which appears quite similar to that reconstructed for the hypothetical ancestor of the genus. Plesiotypic members of the *D. semisulcatus*- and *D. dimidiatus*-groups show some but not extreme modification from the ancestral type. In the *D. marginalis*- and *D. dauricus*-groups, the common presence of an apical knob places them as quite derived from the ancestral type.

Parallel, dramatic changes in form of the apex of the median lobe characterize species in the *D. hybridus*- and *D. semisulcatus*-groups. A high degree of differentiation is found in members of the *D. dimidiatus*-group as well. The *D. marginalis*- and *D. dauricus*-groups show comparatively less within-group differentiation, and yet the presence of the apical knob is certainly a strong isolating mechanism between these two groups and the four more plesiotypic groups.

In summary, there is a transformation series shown by the species-groups of *Dytiscus* in the form of the apex of the median lobe. This series is disguised by within-group changes, and is apparent only after examination of the plesiotypic forms within each species-group. That the plesiotypic member of each group exhibits a form of median lobe most similar to a hypothetical ancestor of that group probably reflects heavy emphasis on the median lobe for construction of the proposed phylogeny, within species-groups, in the first place! The same is not true, however, for comparisons between groups, where, as mentioned elsewhere, other characters such as form of the metacoxal precesses were more heavily weighted.

4.4 Evolution of Dytiscus: Ecological aspects

4.4.1 Introduction

The adaptive zone of members of *Dytiscus*, as for most dytiscids, is that of an active swimming predator which moves vertically through the water column. Adults of *Dytiscus* have more of a lateral component to their movement within the water column than do larvae. Larvae and adults must regularly visit the water surface for respiration. This adaptive zone imposes certain restrictions and allows certain adaptive opportunities in the life history of members of *Dytiscus*.

The purpose of this section is to explore some of these ecological restrictions and opportunities, particularly as they relate to evolution of selected species of *Dytiscus*. A discussion of the systematics of *Dytiscus* can be considered holistic only if it incorporates a reconstructed phylogeny, knowledge of earth history, paleontological information (if available), and consideration of morphological and ecological aspects of the evolution of this group (see Allen and Ball 1980:557).

Most of the ecological relationships discussed here are preliminary hypotheses. The natural history information presented here for the Nearctic species is based on my own fieldwork, except where noted. This discussion is biased toward Nearctic species because of first-hand experience with them. These relationships must be considered as preliminary hypotheses because of the nature of the method by which the information was procured. As a taxonomist, most of my collecting or sampling is qualitative. I have not subjected any of my hypotheses to rigorous quantitative analysis, nor have I collected the information in a manner which would allow such analysis. I have simply thought about where and how I collected the specimens, and tried to formulate patterns from these observations. These patterns form the hypotheses about natural history of species of *Dytiscus* presented below. Although not rigorously analyzed and tested, I offer these patterns here both as suggestions for further study of the natural history of *Dytiscus*, and as preliminary explanations of other features of evolution within this genus.

In the following sections, I first present some information about general features, such as food, discuss some aspects of way of life of *Dytiscus*, Dytiscini, and Cybisterini relevant to these general features, and conclude with a comparative analysis of features of the D. *verticalis*- and D. *hybridus*-groups. This discussion is restricted to these groups because they are plesiotypic within *Dytiscus*, and are exclusively Nearctic groups so that I have field experience with all member taxa except D. *habilis*.

4.4.2 General Features

4.4.2.1 Food

At most localities where I have collected specimens of *Dytiscus*, food did not appear to be a limiting factor in determining beetle abundance. Larson (1975:395) observed that tadpoles were the most common prey of larval *Dytiscus* in Alberta. I, however, found gammarids (which were vigourously eaten by laboratory reared larvae) to be the most abundant prey animal at sites where larvae were common. The number of prey organisms required for larval development is amazing. For instance, Blunck (1924:726) showed that development of third instar larvae of D. *marginalis marginalis*, at a constant temperature of 17-18°, could be completed in as little as 15 days, but only by consuming 27 tadpoles of 25 mm length per day. Also, Blunck demonstrates that duration of larval stages was dependent on number of prey available, given a constant temperature. Third stage larvae, reared under conditions similar to those above, commonly required in excess of 50 days if fed fewer than three tadpoles per day.

The range of acceptable prey of adult and larval *Dytiscus* is extremely wide (Wilson 1923, Blunck 1924:630-637, Galewski 1971), consisting of any animal large enough for them to handle and which attracts attention by quick movement. This includes larvae of the same and other *Dytiscus* species. The overall aggressiveness of larvae is well demonstrated by the recent observations reported by Drummond and Wolfe (1981) of a third instar larva of *D. marginicollis* killing a 192 mm long neonatant garter snake.

4.4.2.2 Predators

In most habitats where they are abundant, species of *Dytiscus* form the top consumers of the food web. The major predators of *Dytiscus* larvae and adults are other specimens of *Dytiscus* and vertebrates such as fish, ducks and geese.

In fish hatcheries, where the fish are of a smaller and uniform size, *Dytiscus* specimens are considered a serious pest (Blunck 1916b, Wilson 1923). In natural situations, larger fish probably constitute very important predators of *Dytiscus* (*e.g.* see Natural History of *D. lapponicus disjunctus*). Collecting experience supports this contention. Specimens of *Dytiscus* are abundant in sloughs of western Canada, which are generally devoid of fish. However, in those sloughs used for rearing trout as a summer crop, *Dytiscus* are abundant in spring, but absent by autumn. Similarly, other water bodies with fish are generally unsatisfactory places for collecting *Dytiscus*.

4.4.2.3 Parasitoids

The general potential role of egg parasitoids in the natural history of *Dytiscus* is well summarized by the following statement by Jackson (1964:95):

> "Only in eggs of *D. marginalis* laid in early spring have I found a complete absence of parasitoids, and the early laying of *Dytiscus* must be an important factor for its survival."

Jackson's suggestion that selection pressure by parasitoids would lead to a trend to early season oviposition implies that activity of adults and development of eggs and larvae would have to take place in increasingly cooler water. Furthermore, if this trend is applicable to members of the whole genus, then more advanced taxa could have distributional ranges exploiting this physiological attribute. Thus selection pressure from egg parasitoids may be preadaptive for life in more northern habitats.

4.4.2.4 Oviposition sites

One important feature of habitats associated with successful propogation of *Dytiscus* is presence of aquatic vascular plants such as *Acorus*, *Iris*, *Alisma*, *Sagittaria*, *Potamogeton*, *Glyceria*, *Scirpus*, and *Typha* (Balduf 1935:37), which are preferred oviposition sites. Choice of these may be due to the oxygen supply provided by the plants to the relatively large eggs characteristic of members of *Dytiscus*

(Balduf 1935:39). The ovipositor of female *Dytiscus* is blade-like and well suited for endophytic egg deposition (Wesenberg-Lund 1912:27-31, Galewski 1971b:513, 615-621). Therefore, reproduction usually takes place in permanent ponds where such plants are found.

Occasionally, larval development will take place in temporary ponds. Wiggins *et al.* (1980:108, 163) and James (1970) have shown that larval development of such species as *D. fasciventris* can be completed in temporary vernal ponds. In such situations, females probably oviposit either into some form of amphibious plant such as *Iris* or into flooded terrestrial plants.

4.4.3 Habitat of origin of Dytiscus and Dytiscini

Members of *Hyderodes* (Watts 1978) and more plesiotypic members of *Dytiscus* (such as *D. verticalis*) are associated with shaded ponds in deciduous forests. In the absence of contradictory information, I assume this to be the habitat of origin of Dytiscini. Occurrence of taxa in other habitats is therefore considered as a derived feature.

4.4.4 Body size and the adaptive zone of Dytiscini and Cybisterini

Among dytiscids only two tribes have members which are consistently in excess of 25 mm in body length. These are Cybisterini and Dytiscini. Presuming that this similarity in body size combined with the common adaptive zone of members of these tribes can be used as a rough guide to niche use, then one prediction which I made and subsequently tested was that the members of one tribe (Cybisterini) could be competitively excluding the other (Dytiscini). Such a generalization applies only within broad limits and is subject to numerous exceptions, particularly with respect to habitat and behavioural specializations. Distributions of these tribes show marked parapatry on a global level (data for Cybisterini from Brinck 1945, and that for Dytiscini from Watts 1978 and the present study). Cybisterini are most diverse on the land masses where Dytiscini are absent. For instance, in Canada the genus *Cybister* is represented by only one species which extends only into the extreme southern portions of Ontario and Quebec (Roughley, unpublished data), whereas *Dytiscus* is markedly diverse in this country. Similarly, Cybisterini are most diverse in Africa where Dytiscini are absent. Based on this information, I predict that individual members of Cybisterini (as a general trend) are competitively superior to members of Dytiscini. Also, it seems logical to suggest that members of at least one of these tribes has relatively recently invaded the niche space (*via* body size) of the other, or that they have recently converged in niche space (*via* body size). This is quite likely, since both groups were present and had their early evolutionary history on southern Gondwanaland. In aggregate, Cybisterini are more diverse than, and show a greater range of body size and other features, suggestive of more evolutionary plasticity, than do the aggregate Dytiscini, and I therefore suggest that Cybisterini have recently invaded the niche of Dytiscini. A modified version of Erwin's (1979:542) taxon pulse is sugested as the mechanism by which the latter took place.

4.4.5 Ecological aspects of D. verticalis- and D. hybridus-groups

4.4.5.1 Body size

Despite problems associated with measurements of adult specimens (Section 2.2.2), it is clear that the five members of these species-groups comprise two groups based on size. Specimens of *D. verticalis* and *D. harrisii* are larger than specimens of *D. hybridus*, *D. marginicollis*, and *D. habilis* (Tables 2 and 7).

4.4.5.2 Habitat characteristics

Characteristics of the habitats of members of these species-groups are summarized in Table 8. All species live in lentic habitats, but specimens of *D. harrisii* also occur in relatively still water within a lotic microhabitat. Three of the other four species (*D. verticalis*, *D. hybridus*, and *D. habilis*) occur in both saline and fresh-water ponds in western North America and adjacent Mexico. In many moderately to highly saline ponds, *D. harrisii* is the only species of large dytiscid encountered.

4.4.5.3 Evolution with respect to habitat

The presumed habitat of origin and therefore preferred habitat of early members of *Dytiscus* was shaded ponds of deciduous forests. In pre-Tertiary times, the broad-leaved deciduous forests covered much of Laurasia (Matthews 1979). Ponds in these forests were occupied by at least two species of *Dytiscus*: one larger and similar to *D. verticalis*, the other smaller and similar to *D. hybridus*. The progeny of these ancestors have retained an affinity for these habitats. The latter were presumably residents of deciduous woodland ponds, because: 1) this is the inferred habitat of origin; 2) the woodland pond habitat has existed longer in North America than the grassland, saline habitat of *D. marginicollis*; 3) the lotic specializations of *D. harrisii* are apotypic and unique to it; and 4) adults of *D. hybridus* and *D. verticalis*, which occur in woodland pond habitats today exhibit many character states believed to be plesiotypic to these clades. These two species, then, have remained in the plesiotypic habitat.

In Table 8, I have characterized *D. harrisii* as occurring in both lentic and lotic macrohabitats. However, in the species treatment of *D. harrisii*, I mentioned the possibility of its preference, at least for larval development, of still or slow-moving backwaters of sluggish streams. Larvae of *D. harrisii* which I have observed both at field sites and under laboratory culture behave differently than other species. The larvae lie flat, parallel to the water surface, whereas those of other species rest in an S-shaped position. I believe this to be an adaptation to lentic portions of the lotic macrohabitat. Such a resting position would reduce the effect of any currents in this habitat. As well, many larvae are found lying among the floating stems and leaves of aquatic plants which are a common feature of this habitat.

Part of the duality of habitat occurrence noted in the species treatment is explained if the original speciation of *D. harrisii* took place in lentic/lotic habitats, but, now having achieved species level divergence, this taxon has re-invaded pond type habitats. The larval behaviour is a remnant of evolution in lentic/lotic habitats.

The phylogenetic position of *D. harrisii* indicates that it is probably derived from an ancestor common with that of *D. hybridus*, *D. marginicollis* and *D. habilis*. This ancestor would have occurred in woodland ponds, and given rise to two sister taxa, one of which has led to *D. harrisii*. I hypothesize that divergence of the ancestors due to ecological specialization of *D. harrisii* took place in the following manner. A high percentage of permanent ponds have outlets. If a certain portion of the ancestor of this group of *Dytiscus* species occurred within the lentic/lotic portion of these outlet areas then a situation where rapid, divergent selection took place could have brought about speciation rapidly, especially if correlated with an increase in body size of *D. harrisii*. Such sympatric speciation by ecological divergence has been demonstrated in other groups (see Futuyma and Mayer 1980, Hammond 1981a)

Although there is evidence that *D. hybridus* remained in the plesiotypic habitat, further observations are needed to secure similar confidence about the habitat preferences of *D. habilis*. The inferred phylogenetic postion of this taxon would suggest its populations have also remained in the plesiotypic habitat. If, however, it is found to be as alkali-tolerant as *D. marginicollis*, then a re-evaluation of its phylogenetic postion and ecological history of this group will be necessary.

The habitat of *D. marginicollis* could have been affected by the uplift of the Rocky Mountains. As the resulting rain shadow spread and conditions became drier in western and southwestern North America, the ancestors of *D. marginicollis* presumably became adapted to more saline habitats on grassland. For instance, if the chemical history of Lake Bonneville (Hubbs and Miller 1948) can be used to generalize the history of ponds in the southwestern United States, the continuing fluctuation between saline and freshwater characteristics may have been slowly exploited by members of *D. marginicollis* until the present day ecological tolerances of this species were achieved.

4.5 Evolution of Dytiscus: Chorological aspects

4.5.1 Introduction

The purposes of this section are to state my interpretations of various theories of biogeography, and to compare explanations of the observed distribution of selected species-groups of *Dytiscus* and Dytiscini. This is justified because each general theory or paradigm has limits, and elements of general theory are incorporated here into a more holistic theory called the synthetic theory. The theories discussed are: dispersal theory (including taxon pulses and competitive displacement); vicariance theory; ecological determinism; and the synthetic theory. Paradigms of biogeography are few, and none of those currently used are new. Most have gone through dramatic changes from time to time as they become popular or in vogue. At such times, these paradigms are revised and revitalized. Testing of a paradigm or theory of biogeography is analysis of relative amount of explanation, correlation and prediction that it makes about phylogenetic and chorological relationships of the taxa under consideration. Various ancillary considerations should be used to establish the probability of one paradigm (or a combination of paradigms) being more correct (*i.e.* of having the highest explanatory, correlative and predictive value) for a specified biota. Among these considerations are mode of speciation, degree of divergence or differentiation, degree of convergence, congruence with other patterns similarly analyzed, state of knowledge of geological and climatic history of area under consideration, consistency between phylogenetic reconstruction and chorological pattern, and relative strength of phylogenetic reconstruction. These considerations are checks and balances to a biogeographic interpretation, and render this type of analysis dependent on other kinds and sources of information. Because of this, a biogeographic scenario for a group may have appreciable value if the proper kinds, sources and amounts of information are used, but at the same time, it suffers the weakness of having to draw on such a broad base of support. For instance, my interpretation of chorological aspects of *Dytiscus* would undoubtedly be very different if it had been written before modern knowledge of plate tectonics was achieved. Similarly, my interpretations would probably be quite different if it were written some time in the future. In order to extend the time that an interpretation is useful, it seems to me that the most effective means is to take into account, as thoroughly as possible, possibilities for cross-checking the information presented by means of the various considerations mentioned above.

My treatment of chorological aspects of *Dytiscus* begins with a brief statement of various paradigms of biogeography which are or could be used in explanation of the pattern. The stimulation to write this section came from the brief synopsis presented by Heyer and Maxson (1982). I have modified the limits they established for some paradigms, extended the discussion of most, and excluded still others (*i.e.* island biogeography) depending on their seeming relative importance in explantion of the zoogeographic pattern shown by *Dytiscus*. I must stress that division into separate theories is, to me, artificial. I have rejected portions of some paradigms and amalgamated the remainder into what I term "synthetic biogeography". It is important to state the degree to which each paradigm is used in the interpretation. Too frequently, I have been attracted to papers which advertise in the title or keywords a particular type of biogeographic interpretation, only to find upon reading the paper, that the analysis provides little information about that particular paradigm.

Subsequent sections present my interpretation or explanation of the observed distribution pattern of genera of Dytiscini and of the species of the *D. verticalis*- and *D. hybridus*-groups. (These groups are treated for the reasons stated in Section 4.4.1.) The zoogeographic recontruction is the most parsimonious explanation of the distribution of extant and fossil members, and the phylogenetic arrangement of members of Dytiscini. Because it is hypothetical, I have avoided overuse of such words as "probably", "presumably" or "possibly" except where I believe re-emphasis of the tentative nature of the reconstruction is warranted. For the same reason, I have stated the corollaries of the hypothesis, for it is in this way that the hypothesis may be tested (Ball 1976).

When reference is made to such areas as "Africa" in earlier geologic time, I refer to the geographic area recognized as that continent today, although in the past, the physical dimensions and relative positions of the continents were quite different from those of today.

4.5.1.1 Dispersal theory

The traditional explanation of this theory involves two major elements: 1) one or more centres of origin, or source areas, and 2) movement or dispersal from this source area. From the centre of origin, sequential dispersals of increasingly advanced taxa spread out (*i.e.* overcome dispersal barriers), and eventually achieve the observed pattern. Successive dispersals or pulses of more advanced taxa competitively displace older, more plesiotypic taxa. Information used from reconstruction of the chorological history of groups are such things as numerical abundance as evidence for the centre of origin, degree of differentiation of taxa, and extent and area of their distribution. Fossils also provide some information about the proposed centre of origin, but provide more information about time of dispersal. The advent of explicit and rigorous methods for reconstruction of phylogenies has allowed incorporation of distribution of sister-groups as well.

The sequential nature of the dispersal theory is well illustrated in the classic study of Wilson (1961), who termed the process the taxon cycle. It represents a more precise compilation of Darlington's (1957) ideas. Erwin (1979) extended the concept of this element of the dispersal theory, and proposed the more appropriate name 'taxon pulse'. Erwin gives many examples and detailed discussion of taxon pulses in the mainland carabid fauna.

Taxon pulses consist of a series of waves of invasions from one or more centres of origin into previously unoccupied regions or habitats. Earlier arrivals occupy generalist habitats, but subsequently invade previously unexploited niches. Later arrivals represent widespread ecological generalists. The mechanism affecting the earlier arrivals is a combination of niche specialization and lower competitive ability so that they become specialists of restricted range. Taxon pulses, then, require dispersal from one or more centres of origin, and differentiation, which eventually results in specialization by means of divergence, accompanied by ecological specialization and displacement by the later arriving ecological generalists. A mainstay of ecological theory is the belief that two species cannot occupy the exact same niche in the same range at the same time. A corollary of this is the prediction and observation that geographical exclusion of one of any pair of species which fulfill these criteria will result (see Arnold 1981 for review). Such displacement operates at the species level by individual interactions, but should be observable at both the species level and at higher taxonomic levels such as the generic level. The latter should only be so if at least some of the species of the genera concerned occupy the same niche. Further discussion of dispersal theories is provided by Darlington (1957), Erwin (1970:184-208), Simpson (1978:153-162) and Udvardy (1981), and references cited therein.

Important weaknesses of this model, cited by its critics, are: 1) reliance on dispersal from centre of origin to achieve observed patterns, 2) lack of explanation of recurrent patterns of distribution called "tracks", 3) rejection of continental drift, 4) rejection of allopatric speciation, and 5) difficulty of testing such hypotheses (*e.g.* Croizat *et al.* 1974, Platnick 1976, Rosen 1978, and Nelson and Platnick 1980). Other defects in the dispersal paradigm are discussed in these papers, but are not considered further here. Most of these criticisms are fallacious for various reasons, and others are misconstrued artifacts of historical perspective. Some of these criticisms are discussed below.

Every biogeographer seeks consistent patterns. This is the very nature of biogeography, and is not dependent on whether or not one proposes major use of dispersal to achieve this pattern (*e.g.* Darlington 1957). At the same time, a summary of attempts to explain all patterns by dispersal can appear chaotic. The map of Handlirsch's (1913 map 5, redrawn in Simpson 1978:154) compilation of all land bridges postulated up to 1913 is informative in this respect. It appears from the map that no generalized patterns have been sought. I think it is more indicative of many different explanations (hypotheses) of many different recurrent patterns. Works for which dispersal was the predominant explanation are legion and it therefore does not seem implausible that many different hypotheses have been erected. However, these are attempts to explain recurrent patterns.

Implied rejection of continental drift is primarily a historical artifact. Previously, dispersal biogeography was hampered by inadequate information about earth history. Because of this, many early dispersal-type hypotheses seem to (and some do) verge on unbridled speculation in light of present knowledge of plate tectonics. Plate tectonics was only accepted by geophysicists after documentation of the 1960's (Marvin 1973). Biogeographic interpretations (taking into account the delay in information crossing interdisciplinary boundaries) appearing before this time did not have available the requisite background information.

Implications of rejection of the allopatric speciation model is partly correct and partly false. The role of barriers in speciation is evident throughout the history of biogeography (*e.g.* Nelson 1978). Other biogeographers have proceeded without a concise definition of the manner in which taxa are formed. Still others, such as Ernst Mayr, have certainly accepted allopatric speciation (1963), as well as disperalist explanations (see quotations of Mayr's work in Croizat *et al*. 1974). Alternatively, the role of other models of speciation, such as sympatric speciation, is becoming increasingly prevalent in systematic studies (*e.g.* Hammond 1981a, b).

Testing of dispersal explanations is possible. The vicariance paradigm predicts that taxa are created by barriers that disrupt previously discontinuous ranges, whereas the dispersal paradigm predicts that taxa originate within certain areas, and subsequently move out of that area by crossing barriers, differentiate, possibly disperse again, *etc*. For instance, the *D. marginalis*-group occurs only in the Palearctic Region, yet members of *D. dauricus*- and *D. dimidiatus*-groups are Holarctic (Fig. 30). A vicariance hypothesis would predict original presence of *D. marginalis*-group in North America, but subsequent extinction there (corroboration provided by discovery of fossils assignable to *D. marginalis*-group in North America). A dispersal hypothesis would predict that *D. marginalis*-group did not occur in North America (falsified by above). Similarly, the dispersal model would predict that any fossil specimens discovered on land bridge routes (*e.g.* North Atlantic or Beringian routes) will be assignable to members of extant, or to near ancestors of extant Nearctic taxa. Modern vicariance biogeographers (*e.g.* Croizat *et al*. 1974:269) espouse the view that the role of dispersal is modification of distribution of taxa created by vicariance. They believe that the only evidence of dispersal is sympatry of species. However, I believe that dispersal of organisms is a common phenomenon. Certainly, no biologist with a knowledge of the biota of glaciated areas (such as Canada), and of the extent of periodic glaciations, is likely to underestimate the power of dispersal. Almost the entire biota of Canada has been derived by dispersal, and this is particularly true of the dytiscid fauna (Larson 1975:412-419). Consequently, the role of dispersal in biogeography is of extreme importance.

A question which remains is the relative role of dispersal in explanation of source(s) of the biota under consideration. Specifically, does the dispersal paradigm explain the origin and source of taxa or only modification of range of already existing taxa? To me, this is a matter of scale. Higher taxa are more diverse in some areas than in others. Presumably, more speciation (allopatric or otherwise) has taken place there. Also, certain ancestral stocks have invaded new geographic areas and diversified within them. Thus, my answer to this question is that dispersal has played a role in adjustment of ranges, and that long-distance (*i.e.* land bridge type) dispersal has at other times provided the "raw material" for subsequent vicariance.

4.5.1.2 Vicariance theory

The following synopsis is distilled from Croizat *et al.* (1974), Platnick (1976), Rosen (1978), and Nelson and

Platnick (1980). I have freely interspersed some implications and inferences required by this theory but not consistently stated by its proponents.

Vicariance biogeography consists of a search for, and analysis of, recurrent patterns of distribution. The primary mechanism of speciation required by the theory is appearance of barriers which divide the continuous range of an ancestral taxon, with subsequent divergence of descendant taxa in isolation. This theory implies stability of communities over long periods of time and that constraints on dispersal are many and rarely overcome. Locations of taxa can and do change. Such implications are required by the recurrent patterns and the degree of stasis and panmixis of taxa within communities necessary for this theory to be effective.

Occurrence of related taxa on presently discontinuous land masses, or in presently isolated habitats on presently continuous land masses, are evidence of previously contiguous ranges of ancestral taxa. Sympatry of ranges of closely related taxa is accepted as evidence of dispersal, however. Vicariance biogeography is not new (Nelson 1978), but became refined and revitalized because of juxtaposition with cladistic analysis. I cannot agree with Heyer and Maxson (1982:404) that "vicariance biogeography is more or less what used to be called allopatric speciation..." Vicariance biogeography is dependent on allopatric speciation, but, as mentioned above, it is possible to accept allopatric speciation while rejecting the vicariance theory. Because vicariance is dependent on allopatric speciation, mode of speciation for the group under study must be understood prior to application of vicariance theory.

Vicariance biogeography is an extension of cladistic analysis of relationship of taxa based on structure, into analysis of relationship of these same taxa based on geographic space. It comprises a unit of phylogenetic inference referred to by some authors as chorological relationships. As such, it was one of the kinds of evidence used by Hennig (1966). Thus, the relationship between phylogenetic position and geographic space of taxa can be used in reciprocation to derive a more rigorous phylogenetic arrangement (Hennig 1966:148, Whitehead 1972:303). Vicariance biogeography shares with cladistic analysis the strengths of ease of hypothesis construction and testing (Ball 1976). It suffers the weakness of compounded hypotheses, assumption of a single mode of speciation, limitations of knowledge of earth history and related phenomena, and, in many studies, a lack of temporal control (*e.g.* fossils) on age of taxa.

I think other weaknesses of strict application of viacariance biogeography come about because of the implied decrease in the role of ecological interaction between taxa, and lack of discussion (lack of explanation?) of such well-known phenomena as the role of taxon pulses in faunation of islands. Adherence to a stable-community concept is not supported by evidence from study of Quaternary insect fossils (*e.g.* Coope 1970), which demonstrate large-scale changes in the range of species and that these are independent of past or present communities. Finally, another weakness is apparent in the observation that vicariance alone does not explain all observed patterns of distribution (Heyer and Maxson 1982).

4.5.1.3 Ecological determinism

This theory predicts that distribution of elements of a biota is determined by physical parameters (Heyer and Maxson 1982:405-406). It represents the antithesis of both dispersal and vicariance theories, because it predicts that organisms occur wherever conditions are suitable for them. Therefore, any historical component to an observed pattern is denied.

It cannot be tested. For instance, even if all ecological conditions are judged to be appropriate in a particular area or habitat for a specific taxon which does not occur there, it is possible to suggest that conditions are not really appropriate. Distribution of taxa does not therefore need to be explained. The most important feature of organismic distribution is discovery of the environmental conditions which limit the ranges of individual taxa. A good example of this kind of analysis is the detailed work of Lindroth (*e.g.* Lindroth 1963). The high number of correlations between limits of distribution and isometric contours of physical parameters is highly suggestive of causality, as Thiele (1977) points out.

Heyer and Maxson (1982:405) suggest that it is possible to view ecological determinism on two levels. One of these is strictly causal, as described above, and, as such, offers nothing to the historical biogeographer. Another level, they suggest, is that of habitat distribution of species correlated with a historical explanation. At this level, I think ecological determinism ceases to exist as an independent theory, and is incorporated into either the dispersal or vicariance theory.

4.5.1.4 Synthetic theory

This model takes into account seven major features: 1) plate tectonics, 2) allopatric speciation as the major but not only mode of speciation, 3) occurrence and use of land bridges in the past and present, 4) correlation of ranges of taxa with ecological parameters, 5) dispersal as an important phenomenon in achieving distribution patterns in both the past and present (as indicated by occurrence of widespread taxa (*e.g. D. circumcinctus*)), 6) taxon pulses, and 7) competitive displacement. The synthetic theory as stated here is not new, nor is it unique, but, to me, this approach explains more of the known aspects of earth history and biology than does any constituent element taken alone.

4.5.2 Zoogeography of Dytiscini

4.5.2.1 Pattern and related information

The tribe Dytiscini is comprised of two genera. *Hyderodes* is dibasic, and occurs in eastern Australia and Tasmania (Watts 1978), whereas *Dytiscus* contains 26 species and is confined to the Holarctic region. The tribe Cybistrini is the sister group to most Dytiscinae, including Dytiscini (Burmeister 1976; Roughley, unpublished data). Unfortunately the inter-relationships of Cybistrini at the generic level have not been studied. Cursory examination of characters and distribution of included genera, presented by Brinck (1945), suggest a widespread Gondwanian distribution with subsequent vicariance due to movement of continental segments.

No fossil Dytiscini are known outside the present range of the tribe. Upper Oligocene fossils of *Dytiscus* from West Germany exhibit the synapotypy of sulcate female elytra characteristic of all species groups of *Dytiscus* except *D. verticalis*- and *D. hybridus*-groups (see discussion in Blunck 1913:31-33 and Guignot 1933:866-872; age of fossil strata follows Borkent 1978 and references cited therein). These fossils provide a minimum age for evolution of this character state; probably it is much older. Crowson (1975) suggested that Dytiscidae arose before the end of the Jurassic. Distributional data from some tribes of Dytiscidae such as Cybistrini (Brinck 1945), Hydaticini (Roughley and

Pengelly 1982), and Matini (Mouchamps 1964) suggest that certain tribes of Dytiscidae were established and widespread on Gondwana prior to the dissociation of parts of that continent. Dytiscids and other related Hydradephaga represent a quite old and zoogeographically informative lineage.

Three distinct groups of Hydradephaga probably share a similar zoogeographic history and are representative of an amphipolar pattern in the nomenclature of Crowson (1980). Two of these are dytiscids: Dytiscini as described above, and Matini with one Nearctic and two Australian genera (Mouchamps 1964, Watts 1978). The third hydradephagan group is the family Hygrobiidae, which consists of a single genus with one European and two Australian species (Zimmermann 1920). I have been unable to find many other examples of exclusively Australian-Holarctic, Australian-Nearctic, or Australian-European disjunctions in the literature. Most taxa which have coincident distributions in these areas have members present in other continents such as South America or Africa. I have found only three similar patterns. The distribution of *Culiseta* (Diptera: Culicidae) is mentioned under 'Enigmatic Distributions' by Mackerras (1970:194). Hammond (1975) and Klimaszewski (1979) discuss distributional and phylogenetic relationships of Holarctic *Gymnusa* and austral *Stylogymnusa* (Coleoptera: Staphylinidae: Gymnusini). Another example, cited by Crowson (1980) is that of the tribes Caenoscelini (Holarctic) and Picrotini (New

Zealand) of the beetle family Cryptophagidae. I believe it is significant that five of the six groups (excluding the cryptophagids) are associated with ponds, or at least bog margins and marsh habitats.

4.5.2.2 Dispersal theory

Darlington (1965) suggested that certain taxa presently occurring in Australia could be derived from southward dispersal of groups with a more northern centre of diversity. These taxa would use tropical Asia and the Indo-Australasian archipelago as a dispersal route. That this process is going on even today is illustrated by Howden (1977), who presented information concerning families of beetles, including dytiscids, found in beach drift in New South Wales, Australia. Unfortunately, Howden did not provide specific level determinations, but these species probably are members of the ecological generalist category typical of dytiscids of Pacific and other similar island groups (Roughley, unpublished data). Wind and water dispersal is important within this generalist category, but appears to play a minor role for such groups as plesiotypic Dytiscini.

The possibility that *Hyderodes* represents a Gondwanian-age invasion from the north cannot be ruled out. That the invasion could be more recent than this seems unlikely for three reasons. First, the Australian representative, *Hyderodes*, posesses a suite of plesiotypic character states

(Table 3). The southward dispersal model would predict that the Australian taxa should be apotypic. Second, no members of Dytiscini are known from the intervening areas of the dispersal route. Third, members of *Hyderodes* are structurally quite divergent from *Dytiscus*. This, in combination with the information about the Upper Oligocene fossil above, argue for long separation of their ancestral stocks. Most reconstructions of the history of Australasia suggest that only relatively recently have these continents and islands come into their present positions relative to one another, certainly not prior to late Miocene-Pliocene (Adams 1981). Thus, it seems unlikely that ancestral *Hyderodes* arrived at the present position of the genus by means of recent dispersal from the north.

4.5.2.3 Vicariance theory

A vicariance explanation of the type of distribution shown by Dytiscini must be based on the assumption that the group was previously much more widespread. The group would have to have been widespread on Pangaea during the early Jurassic. Subsequent sequential rupture of this supercontinent into its various plates produced a vicarious pattern with lineages of Dytiscini present on Africa, Antarctica, Asia, Australia, Europe, India, Madagascar, New Guinea, New Zealand, North America, South America, and Tasmania (*i.e.* a pattern similar to that of Platnick 1976:104-105). This system proposes extinction of Dytiscini on all presently unoccupied land masses (*i.e.* Africa, Antarctica, India, Madagascar, New Guinea, New Zealand, and South America). Subsequent evolution of the remaining northern or Laurasian stock led to formation of the genus *Dytiscus*, while the southern or Australian stock led to the genus *Hyderodes*.

This is a relatively strict or narrow interpretation of the vicariance theory. The reconstruction is testable by means of the predictions that it makes that evidence of early Dytiscini will be found on the unoccupied land masses either in the form of presently unknown extant species, or of fossil specimens assignable to Dytiscini.

On the basis of presently available information, I reject this hyopothesis for three reasons. First, no data suggest that Dytiscini occurred on these unoccupied land masses. Second, the number of extinctions on presently isolated land masses demanded by this hypothesis seems inordinately high. Third, and certainly the weakest argument, is that other taxa existing during the same presumed time frame and having undergone the same presumed vicariance have not disappeared from all of these unoccupied land masses (*e.g.* see summary of numerous relationships presented by Humphries 1981).

4.5.2.4 Synthetic theory

My explanation of the present distribution is as follows. Dytiscini originated in temperate southern Pangaea.

They have always been adapted to temperate forest ponds. They dispersed to Laurasia by way of a narrow corridor containing eutrophic ponds in lowland temperate forest. Dispersal to South America, Madagascar, *etc*. was not possible because of mountain ranges or similar areas of inappropriate habitats. Cybistrini arose in southern Pangaea in areas other than those occupied by Dytiscini, or, if they were present in the same area, they were not in competition with them. Cybistrines later invaded the niche of Dytiscini and replaced them in tropical Africa, or, Dytiscini were already absent because of a return to a less temperate climate in Africa. The dytiscine stock survived in temperate areas in the north and *Hyderodes* was either initially protected from cybistrine competition by the breakup of Pangaea, or, Australian cybistrines were at that time not in competition with *Hyderodes*. Although extant *Dytiscus* has been protected from cybisterine pressure by its adaptation to temperate conditions, *Cybister* has now entered the north, and competition may be underway at present.

With respect to the similar patterns mentioned above, what are the chances of finding six groups which show only a Laurasian-Austral disjunction, do not occur on any other land mass, and with five of these six restricted to lentic aquatic habitats? Applying the reasoning of Rosen (1978), the probability is at least less than 1% due to chance, and this is highly suggestive of a common relationship. Similarly, the chances of all of these groups becoming extinct on all unoccupied land masses seems prohibitively high, yet this is the prediction made by uniform application of strict vicariance.

I believe an alternative explanation of this phenomenon, such as that above, which incorporates more of the known earth history and life history of these groups would be of more value. Therefore, I have used the synthetic theory to explain it. Similarly, with particular reference to the number of independent extinctions required by the strict vicariance hypothesis above, I think a hypothesis based on a synthetic theory is more parsimonious and is more easily tested.

This hypothesis predicts that an ancestral stock of Dytiscini was present on Gondwana and widespread only on the southern, temperate portion of the continent. The separation of the African and Australian plates was the event which separated the ancestral stock into lineages which would lead to *Dytiscus* and *Hyderodes*. It predicts that Dytiscini were prevented from colonizing such land masses as South America by barriers, and the present pattern was achieved by northward dispersal of *Dytiscus* along a temperate corridor. Upon attainment of Laurasia, this stock survived, flourished and diversified there.

Perhaps one of the most common patterns used in vicariance biogeography is that of phylogenetic and chorological relationships of taxa found in Australia, southern South America and southern Africa (see summary in

Humphries 1981). This vicariance pattern has been studied for terrestrial groups associated with temperate forests and aquatic groups associated with cool, usually mountain, streams (*e.g.* Chironomidae and Blepharoceridae: Diptera, Ephemeroptera, Plecoptera, and Trichoptera; see Winterbourne 1980 for review). In this regard, the relationships of Dytiscidae are interesting. A comparison of the fauna of southern South America (Zimmermanm 1920) at the generic or subgeneric level to that of the Australian (Watts 1978) or New Zealand (Ordish 1966, 1967) faunas reveals a striking dissimilarity. However, the fauna of southern Africa is much more similar to that of, at least, Australia. Members of Dytiscidae prefer lentic habitats, usually in the form of ponds. Species of dytiscids which live in running or lotic waters are few and are restricted to quiet backwaters or similar areas sheltered from direct effect of current. Therefore, they make use of lentic microhabitats within lotic macrohabitats (Roughley, unpublished data).

> Brundin (1966:452) discusses an Upper Jurassic "...continuous fold-mountain belt roughly corresponding to present New Zealand, West Antarctica, the Scotia Arc, and South Chile, but probably also including now sunken Pacific fore islands. The dynamic arc formed the southern margin of Gondwana and was situated in a moist temperate climate."

Such a continuous montane arc provided with an altitudinal gradient would have provided opportunity for dispersal of terrestrial and lotic-adapted biota, prior to breakup of Pangaea. On the other hand, such an unglaciated mountain chain would have few suitable habitats for lentic-adapted biota. Such lentic habitats, which could have existed within these montane regions, were presumably more oligotrophic than lentic habitats at lower elevations, and thus would provide less than optimum habitats for obligate predators such as members of Dytiscini. This is particularly reinforced if southern Gondwanaland was at higher latitudes than at present (Harrison 1965). Three inter-related features of dytiscine life history suggest that such a mountain chain could have represented a barrier, effectively limiting dispersal prior to breakup. These are: presumed habitat of origin, information about invasion of oligotrophic habitats occurring late in evolutionary history of *Dytiscus* and the recent effects of mountains on distribution and vicariance of species of *Dytiscus*. For instance, in the species treatment of *D. hybridus*, the gap in distribution records for the Appalachian Mountains was noted, and the uplift of the Rocky Mountains in western North America is believed to have formed the barrier separating the common ancestor of *D. fasciventris* and *D. hatchi*.

In summary, early members of Dytiscini were excluded from most of southern Gondwanaland by means of the same mountain chain which acted as a corridor for other taxa.

This hypothesis will be falsified by discovery of information predicted by the vicariance hypothesis. Separation of the African and Australian plates in the later Jurassic separated the ancestral stocks of *Hyderodes* and *Dytiscus*. This analysis has the ancestral stock of *Dytiscus* in southern Africa, while the present distribution is Holarctic, so the next step is explanation of present distribution and elimination of this stock from Africa'.

Crowson (1980) proposes two explanations of amphipolar vicariance: 1) similar to that mentioned above under vicariance hypothesis, *i.e.* extinctions in areas where these taxa do not occur today, and 2) these groups have always been limited to cool-temperate habitats and have crossed the tropics along corridors or during periods of cooler climates. Cool-temperate habitats were presumably widespread throughout tropical latitudes during at least the late Cretaceous based on lowered sea temperatures at the equator given by Pearson (1964). If these widespread cool-temperate habitats existed and were of extensive size for a sufficient period of time, then the ancestral stock of *Dytiscus* (as well as that of other groups mentioned above and in Crowson 1980) may well have followed a lowland dispersal corridor across the present day tropics of Africa and reached Laurasia. This corridor would of course be narrow enough (*i.e.* have an eastern and western barrier) to prevent

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'Certain extant species such as *D. circumflexus* do occur in northern or Palearctic Africa, but this is almost certainly a secondary, perhaps Pleistocene, phenomenon.

dispersal into South America and Madagascar, and therefore is similar to that proposed by Noonan (1973:476, Fig. 247, for the carabid genus *Crassodactylus*).

Absence of plesiotypic members of Dytiscini from present-day Africa may have been brought about by a variety of causes. Subsequent to the cooler climatic conditions referred to above, a warming of tropical latitudes would reduce the aereal extent of and eventually eliminate, the cool-temperate biota and habitats necessary for their continued existence in southern and central parts of Africa. The ancestral members of Dytiscini may also have been excluded from Africa by competition from members of Cybistrini (see Ecological Aspects).

4.5.3 Zoogeography of clades of Dytiscus

4.5.3.1 Introduction

Cladistic relationships and distribution of species of *Dytiscus* is shown in Figure 30. Zoogeography of some individual species-groups is treated elsewhere. Distribution of species-groups allows hypotheses to be made concerning timing and mode of origin of these various component groups. Three possible hypotheses are presented for the derivation of this distributional pattern: vicariance, dispersal, and synthetic. All three of these models predict that, within the *D. semisulcatus*-group, the Nearctic species form a monophyletic unit and that this unit demonstrates a sister-group relationship to at least one Palearctic species in the group (they are and do). The models predict that the Nearctic species of the *D. dimidiatus*-group have a sister-group relationship to all Palearctic members of this group (they do).

4.5.3.2 Dispersal theory

A modified version of dispersal (*i.e.* allowing continental drift, *etc.*) predicts that the centre of evolution for *Dytiscus* was most likely the Palearctic region. The Nearctic fauna is derived by successive invasions of the following stocks: ancestor of *D. verticalis*-group, ancestor of *D. hybridus*-group, single ancestor of the three Nearctic species of the *D. semisulcatus*-group, ancestor of *D. cordieri*, and ancestor of the one endemic Nearctic species of the *D. dauricus*-group. The occurrence of two modern Holarctic species would be due to recent dispersal and represent a modern analogue of previous invasions.

Dependent corollaries of this interpretation are occurrence of between two (*D. verticalis-* to *D. dimidiatus*-group all using one and *D. dauricus*-group another) and five (one each for all species groups occurring in Nearctic) dispersal corridors. It predicts occurrence of widespread taxa on areas recently connected by land bridges (*i.e.* Holarctic species).

This hypothesis is more easily tested by isolated pieces of information, such as may be represented by a fossil site. For instance, co-occurrence of members of two species-groups at the same time on the same dispersal corridor would negate this hypothesis. This model predicts that members of each clade should appear in different strata and therefore occurrence of predicted fossils in transposed strata would also negate this hypothesis. The dispersal theory predicts that any fossil found on a dispersal corridor will be assignable to an existing or to an extinct species-group, but not show characteristics intermediate between two existing species groups. Similarly, this model would be corroborated if sequential distribution of lineages were found.

4.5.3.3 Vicariance theory

Applying strict principles of vicariance to the pattern illustrated in Figure 30, and because all but the *D. marginalis*-group occur in both the Nearctic and Palearctic regions, then all clades would have to have been present on Laurasia before the break-up of that continent into the two component realms. Thus, this hypothesis would demand that each ancestral stock of the individual clades be present and differentiated by at least 80 million years ago. Other dependent corollaries of this hypothesis are: extinction of *D. marginalis*-group in the Nearctic Region; and extinction of *D. verticalis*-group and *D. hybridus*-group in the Palearctic Region. The only unexplained feature of the distribution pattern is that of two Holarctic species, and presumably this would be due to dispersal.

Testing this hypothesis is not easy. No single easily obtainable piece of information (*e.g.* fossil locality) can falsify this hypothesis. This model predicts that fossils of all clades should occur in both zoogeographic regions. Strong support for this hypothesis would come from discovery of a fossil taxon assignable to the *D. marginalis*-group in the Nearctic region.

4.5.3.4 Synthetic theory

My interpretation of the history of clades of *Dytiscus* is as follows. Members of at least *D. verticalis*-, *D. hybridus*-, and *D. semisulcatus*-groups were present on Laurasia prior to 80 million years ago. The major vicariant event splitting each of these lineages was the separation of North America from Eurasia. This arrangement suggests extinction of the former two species groups in the Palearctic region and that fossils assignable to these groups must occur there.

The *D. dimidiatus*-group is more problematic because of the single North American species which possesses a number of plesiotypic character states and represents the sister-group to the Palearctic component of this species group. The qualitative divergence of *D. cordieri* from the remainder of the group is rather large and is perhaps suggestive of long isolation of the respective components. This could be explained if an early member of this clade were widespread between North America and Eurasia before the end of the Eocene. This hypothesis suggests that fossils exhibiting character states attributable to an ancestor of the *D. dimidiatus*-group should occur on the area which formed these North Atlantic land bridges (see Matthews 1979). This hypothesis will be falsified if Nearctic fossils are discovered which are judged to be closer to the Palearctic complex within the *D. dimidiatus*-group.

The *D. marginalis*-group did not reach North America except possibly by introduction by man. In the discussion of taxonomic notes of *D. cordieri* I interpret all previous records of *D. marginalis* as mislabelled specimens or perhaps of a short-lived introduction of this species. If human introduction can be eliminated and recent (or fossil) specimens of *D. marginalis* or *D. marginalis*-group are found in North America, this hypothesis will be falsified.

The *D. dauricus*-group embraces two Holarctic (*D. dauricus* and *D. circumcinctus*), one Nearctic (*D. alaskanus*) and six Palearctic members (Fig. 30). *D. alaskanus* represents the sister-group to a set of species whose total range is Holarctic, but the majority of these are eastern Palearctic. Therefore, the ancestor of *D. alaskanus* could not have entered North America via Beringia before about 70 million years ago, but the invasion probably occurred much more recently than this maximum age.

4.5.4 Zoogeography of D. verticalis- and D. hybridus-groups

4.5.4.1 Introduction

At this point, I drop the system for discussing the various zoogeographic paradigms used above. In part, this is because at the species group level these begin to converge, and also because those two groups are exclusively Nearctic. My analysis of these groups falls under the synthetic theory, but with more reliance on vicariance aspects.

The distribution of the five species in these groups is summarized in Fig. 31, and their habitat affinities in Table 8. In terms of distribution, *D. verticalis* is exclusively eastern, *D. marginicollis* is western, *D. habilis* is Mexican, leaving only *D. harrisii* and *D. hybridus* as widespread species significantly overlapping in range with every other species except *D. habilis*.

I think that most (*i.e.* except *D. harrisii*) speciation events in the history of *Dytiscus* have been allopatric. This is based on three types of information. 1) Specimens of *Dytiscus* are large for insects and possess relatively greater powers of flight. As well, there is some evidence (Table 4) that a feature of their life cycle is both a vernal and an autumnal dispersal flight. These would tend to increase the likelihood of genetic mixing both within and between populations. 2) There is a high degree of correspondence of chorological and phylogenetic position (of both extant and inferred ancestral species) with known palaeogeological evidence which could have provided the barriers necessary for allopatric speciation. These barriers are commonly in the form of disjunctions in preferred habitats (*D. habilis* – *D. hybridus*) or mountain ranges (*D. marginicollis*). The importance of such habitat affinities and of mountain barriers is discussed above.

3) If allopatric speciation is the major mode of speciation and assuming that little ecological divergence occurs subsequently, then the expected pattern would be an assemblage of "vicarages" or ecological-geographical replacement. This is exactly the pattern shown by *D. hybridus*, *D. marginicollis* and *D. habilis*. This pattern of geographical replacement presumably is common within clades because speciation events separating them are relatively more recent, thus providing less time for ecological divergence.

4.5.4.2 Synthetic theory

The pattern of distribution and many details relevant to this discussion are discussed under Ecological Aspects. Therefore, this section only briefly dicusses the vicariance aspects of speciation within the group. Specimens of *D. verticalis* and *D. hybridus* prefer the habitat of origin of the genus. As well, the sympatric divergence of *D. harrisii* is discussed in that section.

A common ancestor of *D. habilis*, *D. marginicollis* and *D. hybridus* occurred in forest pond habitats throughout eastern North America prior to the Miocene. Subsequent vicariance of ancestral *D. habilis* from the common ancestor of *D. hybridus* and *D. marginicollis* could have occurred because of development of a Miocene grassland barrier between forests of eastern North America and Mexico (Rosen 1978, Roughley and Pengelly 1982).

The common ancestor of *D. marginicollis* and *D. hybridus* probably lived on both sides of the slowly uplifting Rocky Mountains during mid-Tertiary times (Rosen 1978). The drier interior of North America created by rain-shadow and other effects of the uplifting Rockies probably divided the range.

This hypothesis may be tested with the following types of information. 1) The phylogenetic arrangement of the members of species-groups is correct and will not be altered by means of testing of the cladogram as new characters and their character states are added to it. 2) Habitat associations as depicted above are based on few specimens. This information is generalized from field notes and laboratory study of these few samples. Is this extrapolation of habitat preference from study of a few specimens valid for the entire species? 3) The occurrence of fossil specimens should be as indicated above.

5. Concluding Statements

The foregoing represents but a preliminary organization of information concerning a group of fascinating beetles. There is much more information needed, particularly concerning structure, function, immature stages, life history, ecological interactions and evolution of species of *Dytiscus*: this, even though, as I stated in the introduction, *D. marginalis* is perhaps one of the most studied species of beetle. Unfortunately, *D. marginalis* is unique in this respect among *Dytiscus* species. Other European species are much less well studied, yet much more is known about them than other Palearctic and all Nearctic species. The problem is the lack of potential for true insights into the evolution of these beetles which would be possible if similar studies on other species were available. This is particularly true of information concerning natural history with which comparisons could be made and used to test the phylogenetic and ecological hypotheses presented above.

Further questions, such as the function of sulcate *versus* non-sulcate elytra of females, pointed *versus* rounded metacoxal processes, importance of large size, *etc.*, are, in my opinion, unsatisfactorily answered in available publications. Answers to these questions could be quite useful in understanding *Dytiscus*, but also may lead to important new interpretations of the evolution of beetles in general, and in aquatic habitats in particular.

Most broadly-based investigations of taxa generate more questions than are answered. This study in no exception. I have answered some questions, but have also, in one way or another, proposed questions which hopefully will lead to the next plateau of understanding.

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Table 1. Comparison of total length, greatest width, and ratio of total length – greatest width (TL/GW) of bottle-trapped specimens of *D. dauricus* Gebler from George Lake, Alberta, and values reported by Larson (1975:403) for specimens captured by unspecified methods. Values are mean ± standard deviation, with ranges in parentheses. Sample size is 28 for both samples. Lengths in mm.

Collecting Method	Total Length	Greatest Width	TL/GW
Bottle trap	34.3 ± 0.8 (33.2 – 36.2)	18.2 ± 0.5 (17.5 – 19.1)	1.91 ± 0.04 (1.88 – 1.98)
Various methods (Larson, 1975:403)	32.9 ± 1.3 (30.0 – 35.0)	16.5 ± 0.7 (15.5 – 18.5)	1.93 ± 0.04 (1.86 – 2.03)
Probability of a larger value for *t*-statistic	$p<0.005$	$p<0.005$	$0.05<p<0.10$

Table 2. Range of measurements (mm) of total length (TL), greatest width (GW), and ratio of total length – greatest width (TL/GW) for specimens of each taxon within *Dytiscus*. TL/GW not necessarily calculated from TL and GW presented here.

	Total Length	Greatest Width	TL/GW
D. verticalis	29.6 – 36.0	16.5 – 19.4	1.79 – 1.86
D. harrisii	32.4 – 39.0	16.4 – 21.9	1.78 – 1.98
D. hybridus	24.2 – 28.1	12.0 – 14.0	1.90 – 2.02
D. marginicollis	26.7 – 33.0	13.4 – 18.7	1.76 – 2.10
D. habilis	23.0 – 27.5	12.2 – 14.1	1.89 – 1.95
D. semisulcatus	22.8 – 31.6	11.6 – 15.7	1.97 – 2.01
D. sharpi	27.3 – 31.0	14.8 – 16.0	1.84 – 1.94
D. carolinus	22.0 – 26.1	11.8 – 14.0	1.85 – 1.92
D. fasciventris	22.0 – 27.9	11.5 – 15.0	1.80 – 2.10
D. hatchi	22.1 – 28.5	11.7 – 15.6	1.83 – 1.95
D. cordieri	26.3 – 32.5	13.6 – 18.1	1.77 – 2.10
D. mutinensis	28.0 – 31.7	14.0 – 16.0	1.98 – 2.00
D. dimidiatus	29.3 – 39.0	15.9 – 20.0	1.84 – 1.95
D. pisanus	28.0 – 33.9	14.6 – 18.0	1.88 – 1.92
D. marginalis marginalis	27.6 – 35.2	15.0 – 17.6	1.84 – 2.05
D. marginalis czerskii	28.7 – 32.6	15.7 – 17.4	1.83 – 1.88
D. persicus	29.3 – 32.4	15.3 – 16.0	1.92 – 2.03
D. delictus	27.5 – 30.6	14.7 – 16.5	1.85 – 1.87
D. latissimus	38.6 – 44.0	23.8 – 28.0	1.55 – 1.62
D. circumcinctus, Nearctic	27.5 – 34.0	13.0 – 17.1	1.80 – 2.10
D. circumcinctus, Palearctic	29.2 – 36.2	14.4 – 17.8	1.95 – 2.09
D. alaskanus	22.6 – 30.2	11.5 – 15.4	1.80 – 2.01
D. dauricus, Nearctic	29.7 – 40.0	15.0 – 20.1	1.86 – 2.03
D. dauricus, Palearctic	27.8 – 33.3	13.9 – 16.6	1.90 – 2.01
D. lapponicus lapponicus	24.1 – 30.0	12.7 – 15.3	1.90 – 1.96
D. lapponicus disjunctus	25.0 – 28.0	13.0 – 14.0	1.92 – 2.00
D. circumflexus	27.0 – 33.1	14.3 – 16.0	1.89 – 2.07
D. thianshanicus	29.3 – 30.5	14.5 – 15.7	1.94 – 2.02
D. latro	29.4 – 31.1	14.8 – 16.1	1.94 – 1.99
D. sinensis	26.5 – 31.0	13.6 – 16.0	1.94 – 1.95

Table 3. Character state matrix for taxa included within the genus *Dytiscus*. Taxa are scored based on the most common state exhibited by specimens examined. Symbols: m = restricted to males, f = restricted to females, - = character absent from taxon.

Character and State Descriptions	*D. verticalis*	*D. harrisii*	*D. hybridus*	*D. marginicollis*	*D. habilis*	*D. semisulcatus*	*D. sharpi*	*D. carolinus*	*D. fasciventris*	*D. hatchi*	*D. cordieri*	*D. mutinensis*	*D. dimidiatus*	*D. pisanus*	*D. marginalis marginalis*	*D. marginalis czerskii*	*D. persicus*	*D. delictus*	*D. latissimus*	*D. circumcinctus*	*D. alaskanus*	*D. dauricus*	*D. lapponicus lapponicus*	*D. lapponicus disjunctus*	*D. circumflexus*	*D. thianshanicus*	*D. latro*	*D. sinensis*
1 Clypeus																												
1.1 Suture																												
1.1.1 linear/curved	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
1.1.2 bisinuate	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
2 Frons																												
2.1 Chevron, extension																												
2.1.1 no	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	1	1	0	1
2.1.2 yes	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0
3 Pronotum																												
3.1 Explanate																												
3.1.1 yes	1	0	0	0	0	1	1	1	1	1	f	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3.1.2 no	0	1	1	1	1	0	0	0	0	0	m	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.2 Anterior yellow band																												
3.2.1 absent	1	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.2.2 present	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3.3 Posterior yellow band																												
3.3.1 absent	1	0	1	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.3.2 present	0	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4 Ventral features																												
4.1 Metepisternum, colour																												
4.1.1 black	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.1.2 black/yellow	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
4.1.3 yellow	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1
4.2 Metasternum, colour																												
4.2.1 black	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.2.2 black/yellow	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1
4.2.3 yellow	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0

continued next page

Table 3. *continued*

	D. verticalis	*D. harrisii*	*D. hybridus*	*D. marginicollis*	*D. habilis*	*D. semisulcatus*	*D. sharpi*	*D. carolinus*	*D. fasciventris*	*D. hatchi*	*D. cordieri*	*D. mutinensis*	*D. dimidiatus*	*D. pisanus*	*D. marginalis marginalis*	*D. marginalis czerskii*	*D. persicus*	*D. delictus*	*D. latissimus*	*D. circumcinctus*	*D. alaskanus*	*D. dauricus*	*D. lapponicus lapponicus*	*D. lapponicus disjunctus*	*D. circumflexus*	*D. thianshanicus*	*D. latro*	*D. sinensis*
4.3 Metacoxa, colour																												
4.3.1 black	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.3.2 black/yellow	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0
4.3.3 black/red	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.3.4 yellow	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	1
4.4 Abdominal sternum I, colour																												
4.4.1 infuscate	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.4.2 yellow	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4.5 Abdominal sterna II-VI, colour																												
4.5.1 black	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.5.2 black/red	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.5.3 black/yellow	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0	0	1	1	1	1	1	0	0	1
4.5.4 yellow	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0
4.6 Metacoxal apex, shape																												
4.6.1 rounded	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.6.2 acute	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
4.6.3 acuminate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
4.6.4 elongate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
4.7 Metacoxal apex, inner margin																												
4.7.1 convex	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
4.7.2 concave	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
5 Elytra, female																												
5.1 Sulcation																												
5.1.1 absent	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1
5.1.2 present	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0
6 Mesotarsus, male																												
6.1 Distribution of palettes																												
6.1.1 evenly distributed	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6.1.2 glabrous area	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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Table 3. *concluded*

	D. verticalis	*D. harrisii*	*D. hybridus*	*D. mariginicollis*	*D. habilis*	*D. semisulcatus*	*D. sharpi*	*D. carolinus*	*D. fasciventris*	*D. hatchi*	*D. cordieri*	*D. mutinensis*	*D. dimidiatus*	*D. pisanus*	*D. marginalis marginalis*	*D. marginalis czerskii*	*D. persicus*	*D. delictus*	*D. latissimus*	*D. circumcinctus*	*D. alaskanus*	*D. dauricus*	*D. lapponicus lapponicus*	*D. lapponicus disjunctus*	*D. circumflexus*	*D. thianshanicus*	*D. latro*	*D. sinensis*
7 Median lobe of male																												
7.1 Lateral ridge, apically																												
7.1.1 present	1	1	0	0	0	1	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7.1.2 absent	0	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.2 Lateral ridge, curvature																												
7.2.1 even	1	1	-	-	-	-	0	-	1	-	-	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
7.2.2 abrupt	0	0	-	-	-	-	1	-	0	-	-	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1
7.3 Pre-apex, laterally																												
7.3.1 linear	1	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.3.2 curved	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7.4 Pre-apex, dorsally																												
7.4.1 parallel	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
7.4.2 sinous	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
7.5 Lateral and dorsal flanges																												
7.5.1 subequal in length	1	1	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7.5.2 dorsal longer	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.6 Tip shape																												
7.6.1 not rounded	1	1	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1
7.6.2 narrowly rounded	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
7.6.3 broadly rounded	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
7.7 Tip shape																												
7.7.1 knob absent	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
7.7.2 knob present	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1
7.8 Tip, well-developed pores																												
7.8.1 absent	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
7.8.2 present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
7.9 Pre-knob, extension																												
7.9.1 absent	-	-	-	-	1	-	-	-	-	-	-	-	-	-	0	0	0	0	-	1	-	1	1	1	1	1	1	1
7.9.2 present	-	-	-	-	0	-	-	-	-	-	-	-	-	-	1	1	1	1	-	0	-	0	0	0	0	0	0	0
7.10 Knob, development																												
7.10.1 moderate	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	1	1	-	1	-	1	1	1	0	0	0	0
7.10.2 significant	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0	0	0	0	-	0	-	0	0	0	1	1	1	1
7.11 Pre-apex dorsally																												
7.11.1 wide	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
7.11.2 thin	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1

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Table 4. List of teneral specimens of selected species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae). (Abbreviated column headings: # = Number and sex of specimens [m = male, f = female]; colln. = collection in which specimens is held [see Section 2.1 for definition of museum codes]).

Taxon / Locality	**Date**	**#**	**Colln.**
D. verticalis Say			
MI, Washtenaw Co., Ann Arbor	27.vii.30	1f	UMMZ
NH, Coos Co., Bretton Wds.	1.ix.24	1f	MCZC
NY, Ulster Co., Ashokan	3.viii.–	1f	AMNH
D. harrisii Kirby			
ONT, Goose Creek, nr. Severn R.	11.vi.56	2f	ROMC
ONT, Pr. Edw. Co.	8.vii.39	1m	UMMZ
ONT, Pr. Edw. Co.	19.vii.39	1f	UMMZ
D. hybridus Aube			
MO, Oregon Co., 12 mi. e Alton	20.vi.40	1m	FMNH
NY, Niagara Co., Olcott	16.vii.22	1m	CUIC
MN, Nicollet Co., St. Peter	24.vii.22	2m, 4f	DEFW
MI, Cheboygan Co., Douglas Lake	–.viii.17	1m	ZSBS
D. marginicollis LeConte			
OR, Marion Co., Salem	31.v.28	1f	USNM
OR, Lane Co., Siltcoos Outlet	7.vi.57	1m	FMNH
BC, Vernon	12.vii.26	1f	CNIC
CA, Amedee	21.vii.28	1m	USNM
ALTA, Medicine Hat	25.viii.25	1f	UMMZ
D. carolinus Aube			
MA, Talbot Co., Wittman	11.v.73	1m	USNM
D. fasciventris Say			
ONT, Belleville	8.vii.63	1f	CNIC
MI, Cheboygan Co.	9.vii.19	1m	UMMZ
NH, Cheshire Co., Jaffrey	13.vii.01	1m	MCZC
ONT, Belleville	22.vii.63	2m	CNIC
MI, Cheboygan Co., Douglas Lake	–.vii.23	1m	DEFW
MI, Cheboygan Co.,	–.vii.35	1m	UMMZ
MI, Alpena Co., Bean Cr.	–.–.25	1f	UMMZ
D. hatchi Wallis			
BC, Smithers	15.viii.51	1m	UBCZ
"	28.viii.49	1m	UBCZ

cont. next page

Table 4. *concluded.*

Taxon / Locality	Date	#	Colln.
D. cordieri **Aube**			
ONT, Belleville	26.vii.63	2f	CNIC
MN, Douglas Co., Alexandria	1.viii.68	1f	SCSU
MAN, Delta Res. Stn., L. Winnipeg	15.viii.50	1f	UBCZ
MN, Saint Louis Co., Duluth	17.viii.42	1m	AMNH
MAN, Winnipeg	28.viii.27	1m	MCZC
D. circumcinctus Ahrens			
BC, Swift Creek, Mt. Robson	10.v.25	1f	UBCZ
SASK, Pasqua	4-18.vi.73	1f	CNIC
NWT, Fort Smith	3.viii.50	1m	CNIC
ALTA, Waterways	12.ix.47	1f	CUIC
D. alaskanus J. Balfour-Browne			
BC, Kamloops	23.vi.41	1m	CASC
"	"	1f	UBCZ
ALTA, Laggan	4.vii.94	1f	AMNH
ONT, Port Arthur	10.vii.65	1m	UGIC
MN, De Sota Lake	21.vii.38	1m	DEFW
NWT, Yellowknife	3.viii.51	1m	CNIC
NFLD, Sandbank Park	19.viii.78	1f	MUIC
NWT, Ft. Resolution	22.viii.47	1m	CUIC
"	"	1f	CNIC
YUKON, Dawson	22.viii.49	1m	CNIC
"	30.viii.49	1f	CNIC
D. dauricus Gebler			
MN, Clearwater Co., Itasca St. Pk.	1.viii.72	1m	ROMC

Table 5. List of specimens interpreted as undergoing dispersal flight, for selected species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae), with label data. (Abbreviated column headings: # = Number and sex of specimens [m = male, f = female]; colln. = collection in which specimens is held (see Section 2.1 for definition of museum codes]).

Taxon / Locality	Date	#	colln.	
D. verticalis Say				
MA, "East Mass."	–.iv.07	1m	USNM	"mouse trap baited with meat"
MN, Stearns Co., St. Cloud	1.v.68	1m	SCSU	lights
IN, Porter Co., Tremont	30.v.27	1f	FMNH	alive in lower beach drift
MI, Washtenaw Co., Ann Arbor	27.vii.30	1f	UMMZ	porch light
MI, Livingston Co., E.S. George Res.	26.vii.41	1f	UMMZ	taken at light
ME, York Co., Old Orchard Beach	14.viii.39	1m	UAIC	at country club on grass
NY, Tompkins Co., Ludlowville	29.viii.64	1f	CUIC	at 15W uv blacklight
CT, Tolland Co., Storrs	26.ix.75	1f	UCSE	migrating
MI, Livingston Co., E.S. George Res.	28.ix.38	1m	UMMZ	taken at light
CT, New Haven Co. Guilford	9–10.x.73	1f	PMNH	uv trap
CT, Litchfield Co., Litchfield	14.x.20	1f	FMNH	house, at lights
MA, Hampshire Co., Belchertown	14.xi.50	1m	UCRC	on tar roof
D. harrisii Kirby				
VT, Chittenden Co., S. Burlington	8.v.68	1f	UVCC	dead on lawn
VT, Chittenden Co., S. Burlington	–.v.68	1m	UVCC	dead in backyard
NWT, Hay River	2.vi.64	1	UCIC	in flight
MN, Stearns Co., St. Cloud	22.vi.72	1m	SCSU	lights
ONT, Pr. Edw. Co.	10.vii.37	1m	CASC	at light
ONT, Chaffeys Locks	13.vii.64	1m	ROMC	uv light
MI, Berien Co., E.K. Warren Pres.	14.vii.20	1f	UMMZ	L. Michigan beach drift
NY, Tompkins Co., Enfield St. Pk.	23.vii.39	1m	USNM	swimming pool
MN, Stearns Co., St. Cloud	26.vii.75	1f	SCSU	at light
MN, Stearns Co., St. Cloud	15.viii.75	1m, 1f	SCSU	at light
WI, Douglas Co., Superior	–.viii.55	1f	SCSU	shore of L. Superior
ALTA, Banff	6.x.81	1f	UASM	in flight

cont. next page

Table 5. *continued.*

Taxon / Locality	Date	#	colln.	
D. hybridus Aube				
IL, Champaign Co., Urbana	14.i.51	1m	INHS	found alive, 7-7.30pm on ground
DC, Washington	28.iii.05	1m	USNM	electric light
NY, Tompkins Co., nr. Dryden	14.iv.67	1m	GWSC	at uv light
IL, Cook Co., Chicago	28.iv.06	1f	UANH	lake beach
DC, Washington	–.iv.–	1f	USNM	electric light
SASK, Regina	18.v.80	1m	UASM	at light
IN, Lake Co., Pine	20.v.06	1f	FMNH	lake beach
IL, Alexander Co., Cairo	10.vi.07	1f	INHS	elec. light
MI, Berrien Co. St Joseph	17.vi.06	1f	FMNH	lake beach
IL, Mason Co. Havanna	28.vi.07	1f	INHS	at light
NY, Tompkins Co., Ithaca	7.vii.25	1m	CUIC	lantern trap
OH, Preble Co., W. Alexandria	7.vii.47	1m	UVCC	in cattle tank
MI, Berrien Co. E.K. Warren Pres.	14.vii.20	4m, 10f	UMMZ	L. Michigan beach drift
MI, Mason Co., Ludington	30.vii.32	1m	FMNH	lake drift
IL, Lake Co., Ill. Beach St Pk.	30-31.vii.75	1m	WUBC	black light
MI, Emmet Co.	27.viii.29	1f	UMMZ	on beach
SD, Brookings Co., Brookings	2.ix.43	1f	UANH	light trap
IL, Peoria Co., Peoria	6.ix.41	1f	INHS	at light, main streets
ONT, Port Credit	–.ix.65	1m	ROMC	uv light
DC, Washington	21.xi.97	1m	USNM	flying
PA, Allegheny Co., Moon Twp.	25.xii.40	1m	ICCM	ground under lighted Xmas tree, pond & small stream ~100 yd away
DC, Washington	12.5.05	1m	USNM	electric light

cont. next page

Table 5. *continued.*

Taxon / Locality	**Date**	**#**	**colln.**	
D. marginicollis LeConte				
CA, Mendocino Co., Mendocino	3.i.55	1f	CASC	flying
BC, Creston	9.iii.53	1m	UBCZ	at light
BC, Vancouver	11.iii.39	1f	CASC	on steps of building
BC, Merritt	15.vi.58	1f	UBCZ	at light
WA, Yakima Co., Toppenish	25.vi.57	1f	OSUO	light trap
UT, Cache Co., Logan Canyon	3.vii.40	1m	EMUS	at light
UT, Millard Co., Oak Creek Canyon	4.vii.37	1m	CASC	at light
"	"	1f	EMUS	at light
WA, Yakima Co., Toppenish	10.vii.56	4m, 4f	OSUO	light trap
OR, Lake Co., 6 mi. ne Plush	12.vii.54	1m, 2f	OSUO	dead on beach
CO, Rio Grande Co., Monte Vista	23.viii.40	1f	DEFW	at light
BC, Salmon Arm	–.ix.35	1m	CASC	flying at light in barn
ALTA, Lethbridge	1.x.29	1	CNIC	flight
CA, Contra Costa Co., Danville	8.xii.48	1m	CASC	at light
D. habilis Say				
CHIHUAHUA, 6 mi w Encinillas, 5420 ft	16.iv.69	1f	UCRC	uv light
AZ, Cochise Co., 5 mi w Portal	–.vi.56	1f	FNYC	swimming pool
CHIHUAHUA, 22 mi w El Sueco	8.x.75	1m	JRZC	tank
D. carolinus Aube				
GA, Clarke Co., Whitehall Forest	9–15.iv.77	1f	RHTC	black light trap
NC, Wake Co.	21.iv.49	1m	CUIC	at light
DC, Washington	4.vi.02	1f	USNM	electric light
MO, Scott Co., Sikeston	16.vi.56	1m	USNM	collected at lights
DC, Washington	13.vii.06	1m	USNM	at light
DC, Washington	4.x.05	1m	USNM	electric light

cont. next page

Table 5. *continued.*

Taxon / Locality	**Date**	**#**	**colln.**	
D. fasciventris Say				
MI, Washtenaw Co., Ann Arbor	13.iv.38	1f	UMMZ	at light
WI, Door Co., Sturgeon Bay	27.iv.71	1m, 1f	WLHC	swimming pool
MA, Middlesex Co., Framingham	29.iv.40	1f	UCSE	in flight, 12 noon
ONT, Dunrobin	28.iv.74	1m, 2f	CNIC	at light
WI, Door Co., Sturgeon Bay	2.v.71	1m, 2f	WLHC	swimming pool
MI, Washtenaw Co., Ann Arbor	19.vi.19	1m	UMMZ	at light
MI, Ottawa Co., Hudsonville	22.vi.77	2f	MSUC	black light
MI, Washtenaw Co., Ann Arbor	24.vi.21	1f	UMMZ	at light
MI, Menominee Co.	24.vi.71	1m	GWWC	electric light
MI, Ottawa Co.	25.vi.71	1f	GWWC	electric light
ONT, Chaffeys Locks	1.vii.64	1f	ROMC	uv light
"	6.vii.64	1f	ROMC	uv light
MI, Cheboygan Co.	7.vii.52	2m	USNM	at light
ONT, Chaffeys Locks	10.vii.64	1f	ROMC	uv light
"	11.vii.64	1f	ROMC	uv light
"	12.vii.64	1f	ROMC	uv light
MN, Itasca State Park	12.vii.37	1f	CASC	at light
MI, Berrien Co., E.K. Warren Pres.	14.vii.20	2m, 4f	UMMZ	L. Michigan beach drift
MI, Cheboygan Co.	14.vii.52	1f	USNM	at light
ME, Lincoln Co., Damariscotta	15.vii.69	1f	CISC	black light
MI, Cheboygan Co., T38 R/E sec.30	16.vii.66	2f	MSUC	uv light
MI, Cheboygan Co., Douglas Lake	16.vii.78	1m, 1f	UASM	beach drift
ONT, Chaffeys Locks	22.vii.71	1f	ROMC	bl. light
PQ, Duparquet	26.vii.44	1f	CASC	at light
PQ, Duparquet	27.vii.44	2m	CASC	at light
ONT, Fraserburg	3.viii.71	1f	ROMC	uv light
MI, Cheboygan Co.	5.viii.52	2m	USNM	at light
MI, Schoolcraft Co., T42N R16W sec.13	6.viii.65	5m, 5f	MSUC	uv light
ALTA, Edmonton	27.ix.70	1m, 1f	UASM	light
ONT Chaffeys Locks	2.xi.69	1f	CNIC	uv light
WI, Waupaca Co., Clintonville	12.xi.39	1m	CNIC	alive on street
CT, Tolland Co., Storrs	6.xiii.73	1m	UCSE	on road

cont. next page

Table 5. *continued*.

Taxon / Locality	**Date**	**#**	**colln.**	
D. hatchi Wallis				
OR, Washington Co., Forest Grove	17.vii.28	1f	OSUO	flying at dusk
CA, Humbolt Co., Arcata	17.vii.69	1m	CISC	black light trap
D. cordieri Aube				
MN, Stearns Co., St. Cloud	30.iii.66	1f	SCSU	lights
"	14.iv.70	1m	SCSU	at lights, cool night
ALTA, Edmonton	18.iv.80	1m	UASM	under street lights
ONT, Guelph	20.iv.75	1m	UGIC	on sidewalk
MAN, Aweme	26.iv.30	1f	CNIC	taken under logs, out of water
SASK, Regina	27.iv.80	1m	UASM	in flight
SD, Brookings Co., Brookings	29.iv.57	1m, 1f	SDSU	light trap
BC, Creston	29.v.48	1m	UBCZ	at light
MI, Wexford Co., Cadillac	10.vii.21	1f	MSUC	in swimming pool
MI, Emmett Co., Big Stone Bay	30.vii.65	1f	UMMZ	beach
ND, Cass Co., Fargo	2.viii.56	1m	NDSU	uv light trap
"	6.viii.56	1f	FNYC	uv light trap
SD, Brookings Co., Brookings	2.ix.43	1m, 1f	UANH	light trap
MN, Stearns Co., St. Cloud	24.ix.69	2m	SCSU	lights
ALTA, Cereal	2.x.70	2-	UCIC	at light
D. circumcinctus Ahrens				
ALTA, Edmonton	18.iv.80	1f	UASM	under street lights
"	27.iv.78	1m, 1f	UASM	in flight
"	24.v.78	1m	UASM	found under doorway light
AK, Fairbanks	4.vii.64	2f	CASC	at electric light, 11:50pm
SASK, Gandview Bch., Last Mtn. Lk.	11.viii.70	2f	ROMC	uv light
ALTA, Edmonton	22.ix.73	1f	UASM	on sidewalk

cont. next page

Table 5. *concluded.*

Taxon / Locality	**Date**	**#**	**colln.**	
D. alaskanus J. Balfour-Browne				
MN, Roseau Co.. Roseau	29.vi.63	1m	DEFW	light trap
SASK, Regina	11.vii.80	1m	UASM	at lights
MN, Pope Co., Glacial Lks. St. Pk.	21.viii.71	1f	DEFW	at black light
D. dauricus Gebler				
MN, Carlton Co., Cloquet	22.iv.58	1m	UASM	at light
PQ, Duparquet	11.vii.43	1m	CASC	at light
ALTA, Edmonton	10.x.73	1m	UASM	at light

Table 6. Distribution of dimorphic elytral states of females of *D. dauricus* Gebler, by political subdivisions of Canada and United States. Based on specimens examined assignable to particular subdivisions.

Province/State	Total Number	Number Sulcate	Proportion Sulcate	Number Non-sulcate	Proportion Non-sulcate
Alaska	78	77	99%	1	1%
Yukon	10	9	90%	1	10%
N.W.T.	13	8	62%	5	38%
British Columbia	20	16	80%	4	20%
Alberta	34	25	74%	9	26%
Saskatchewan	1	1	100%	0	0%
Manitoba	21	9	43%	12	57%
Ontario	7	4	57%	3	43%
Que., N.B.	7	7	100%	0	0%
P.E.I., Nova Scotia	5	5	100%	0	0%
Newfoundland	18	13	72%	5	28%
Wash., Oregon	10	10	100%	0	0%
California	18	18	100%	0	0%
Idaho, Montana	6	6	100%	0	0%
Nevada, Utah	11	11	100%	0	0%
Wyoming	5	4	80%	1	20%
Colorado	8	4	50%	4	50%
N., S. Dakota	2	2	100%	0	0%
Wis., Mich., Minn.	18	18	100%	0	0%
Vermont, New York	4	4	100%	0	0%
N. Hamps., Maine	19	19	100%	0	0%
TOTAL	315	270	86%	45	14%

Table 7. Number of changes of state (derivation of apotypic state or reversal to plesiotypic state) for the 19 characters used for phylogenetic reconstruction of the genus *Dytiscus* Linnaeus. All characters are scored as if existing in two states only. Based on Table 3 and Figure 30.

	Changes of State					
Character	1	2	3	4	5	6
A	X					
3.1	X	X				
4.5′	X	X				
4.5″	X	X	X	X	X	X
4.6	X					
4.7	X					
5.1	X	X	X			
6.1	X					
7.1	X	X	X	X		
7.2	X	X	X			
7.3	X	X	X	X		
7.4	X					
7.5	X	X	X	X		
7.6	X	X	X	X	X	
7.7	X	X	X	X		
7.8	X					
7.9	X					
7.10	X					
7.11	X	X				
Total number of characters undergoing given number of state changes	8	3	2	4	1	1

Total number of state changes = 46.

Table 8. Summary of ecological, chorological and size characteristics of members of the Nearctic *Dytiscus verticalis*– and *D. hybridus*–groups. Filled symbols indicate predominance within the category, open symbols indicate occasional occurrence.

	Size		Distribution			Macrohabitat		
Taxon	**Larger**	**Smaller**	**Eastern**	**Western**	**Mexican**	**Lotic**	**Lentic**	**Comments on habitat**
D. verticalis	●		●				●	ponds in eastern deciduous forest
D. harrisii	●		●	●		●	●	ponds and backwaters of slow streams
D. hybridus		●	●	○			●	ponds in deciduous and mixed forest
D. marginicollis		●		●	○		●	saline and fresh–water ponds
D. habilis		●		○	●		●	unknown–inferred to be forest ponds

Figure 1. Dorsal view of the body of species of *Dytiscus* L. A) *D. verticalis*, B) *D. harrisii*, C) *D. habilis*, D) *D. hybridus*. Scale bar represents 5 mm.

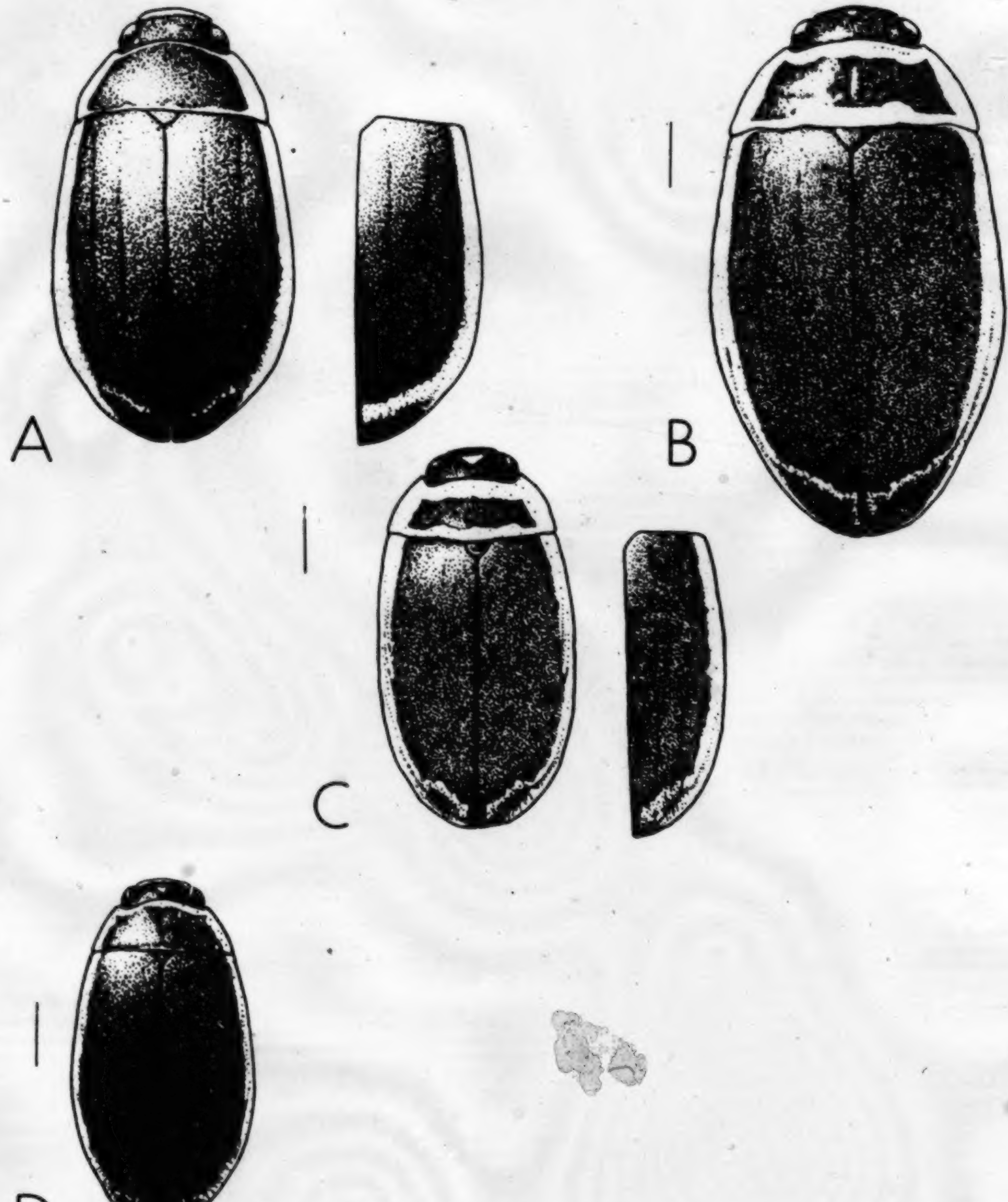
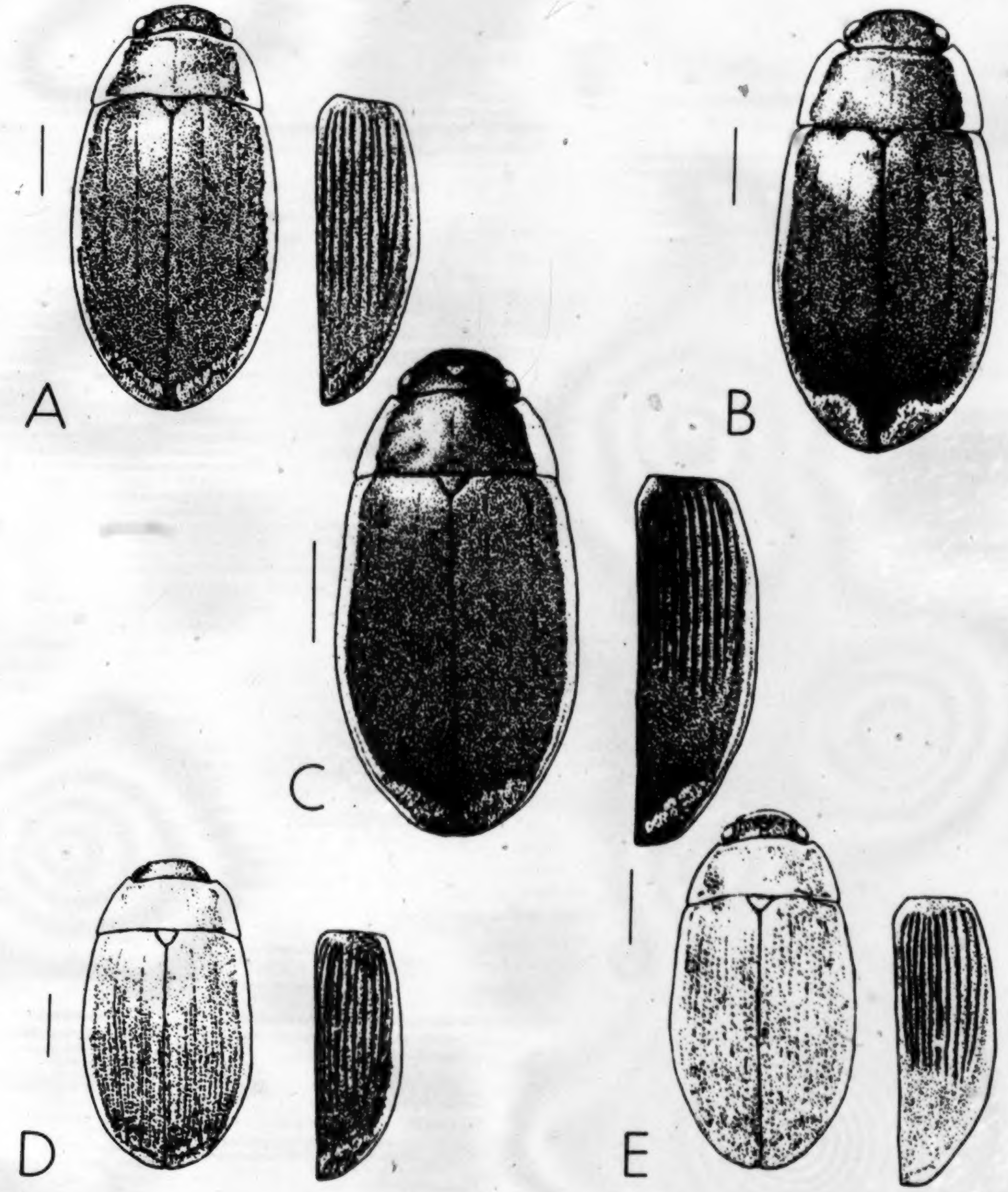

A
B
C
D

Figure 2. Dorsal view of the body of species of *Dytiscus* ~~L~~.
A) *D. semisulcatus*, B) *D. sharpi*, C) *D. carolinus*,
D) *D. fasciventris*, E) *D. hatchi*. Scale bar represents 5 mm.


A
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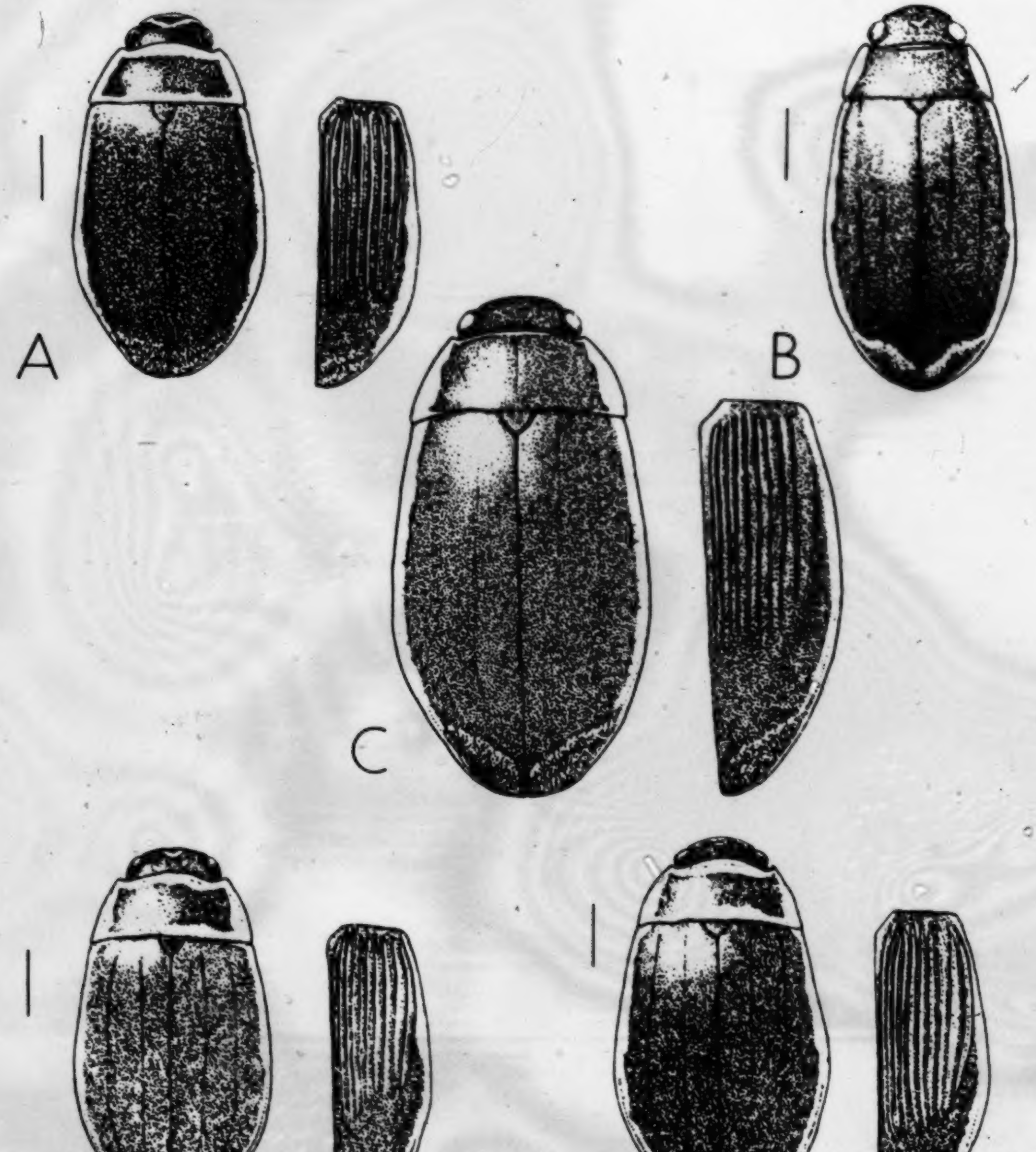
E

Figure 3. Dorsal view of the body of species and subspecies of *Dytiscus* L. A) *D. cordieri*, B) *D. mutinensis*, C) *D. dimidiatus*, D) *D. pisanus*, E) *D. marginalis marginalis*. Scale bar represents 5 mm.


A
B
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D
E

Figure 4. Dorsal view of the body of species of *Dytiscus* L. A) *D. delictus*, B) *D. latissimus*, C) *D. circumcinctus*. Scale bar represents 5 mm.

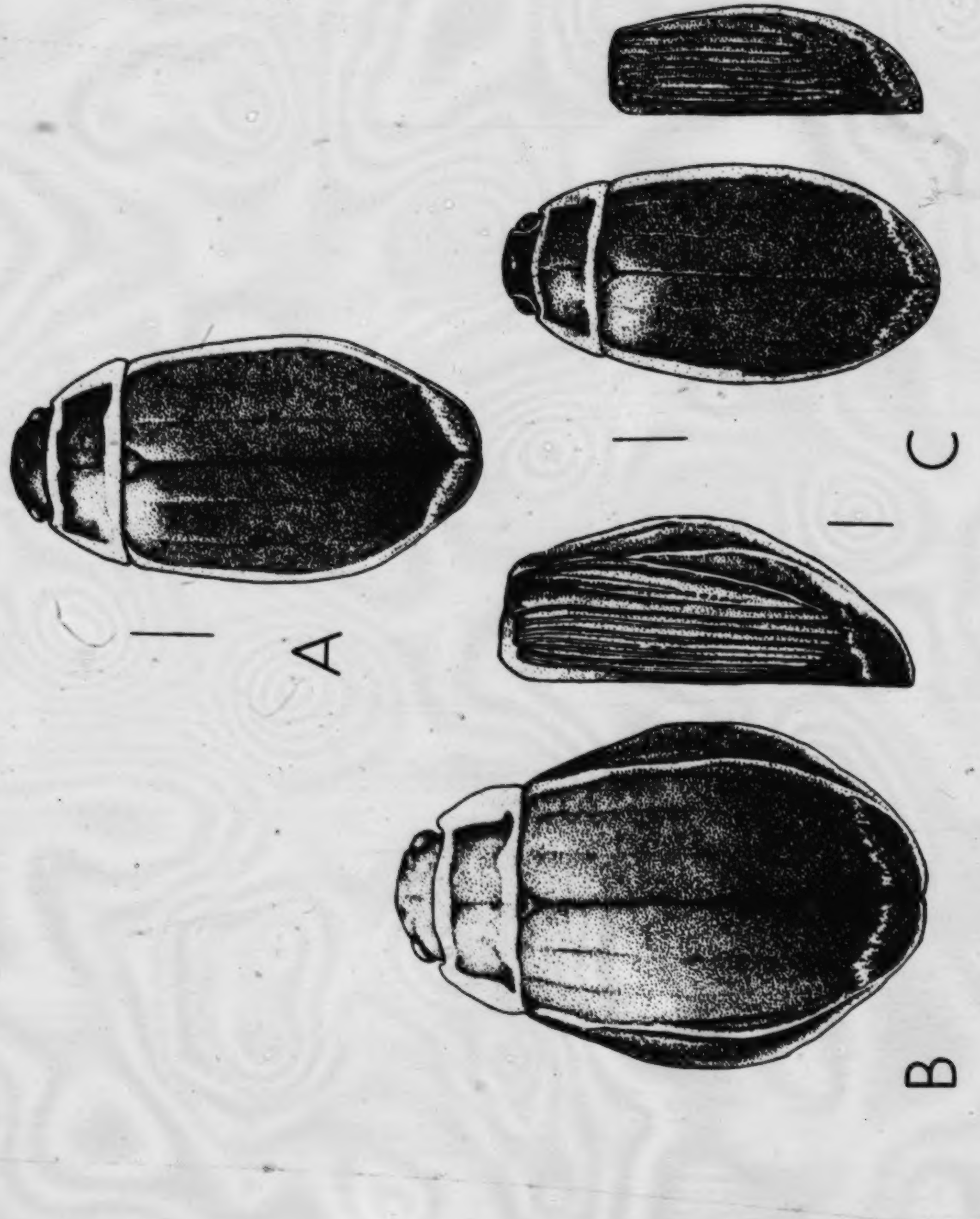
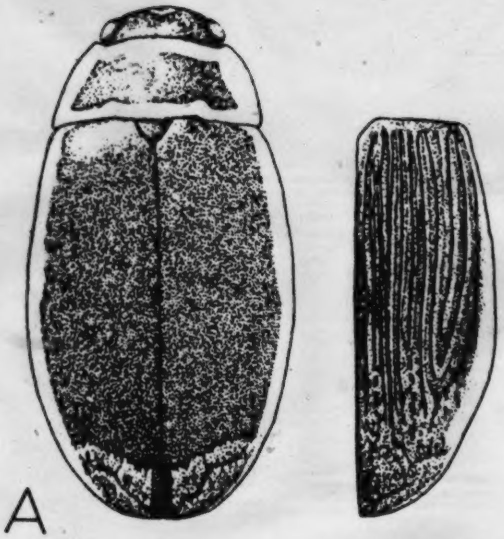
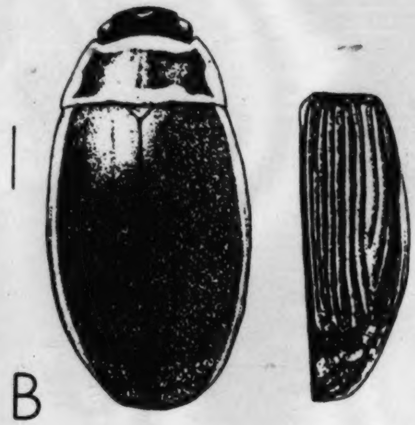

A
B
C

Figure 5. Dorsal view of the body of species and subspecies of *Dytiscus* L. A) *D. alaskanus*, B) *D. dauricus*, C) *D. lapponicus lapponicus*, D) *D. circumflexus*, E) *D. thianshanicus*. Scale bar represents 5 mm.



A



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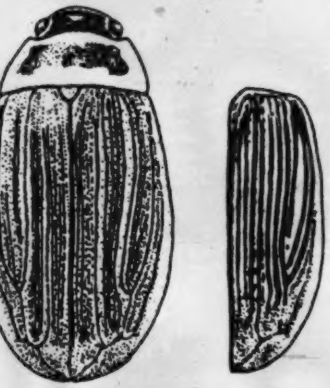
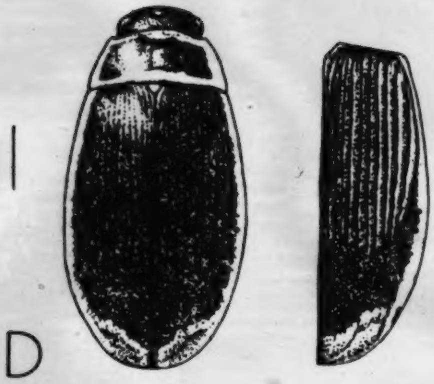
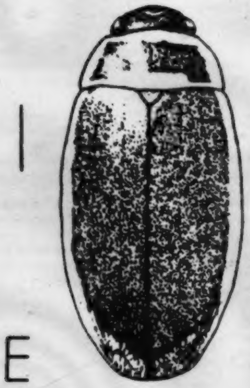


C

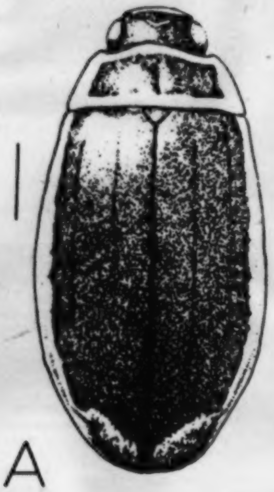


D



E

Figure 6. Dorsal view of the body of species of *Dytiscus* L. A) *D. latro*, B) *D. sinensis*. Scale bar represents 5 mm.


A

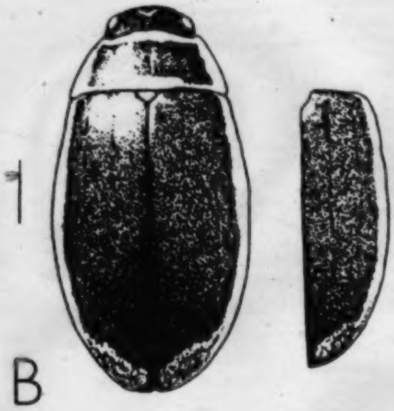
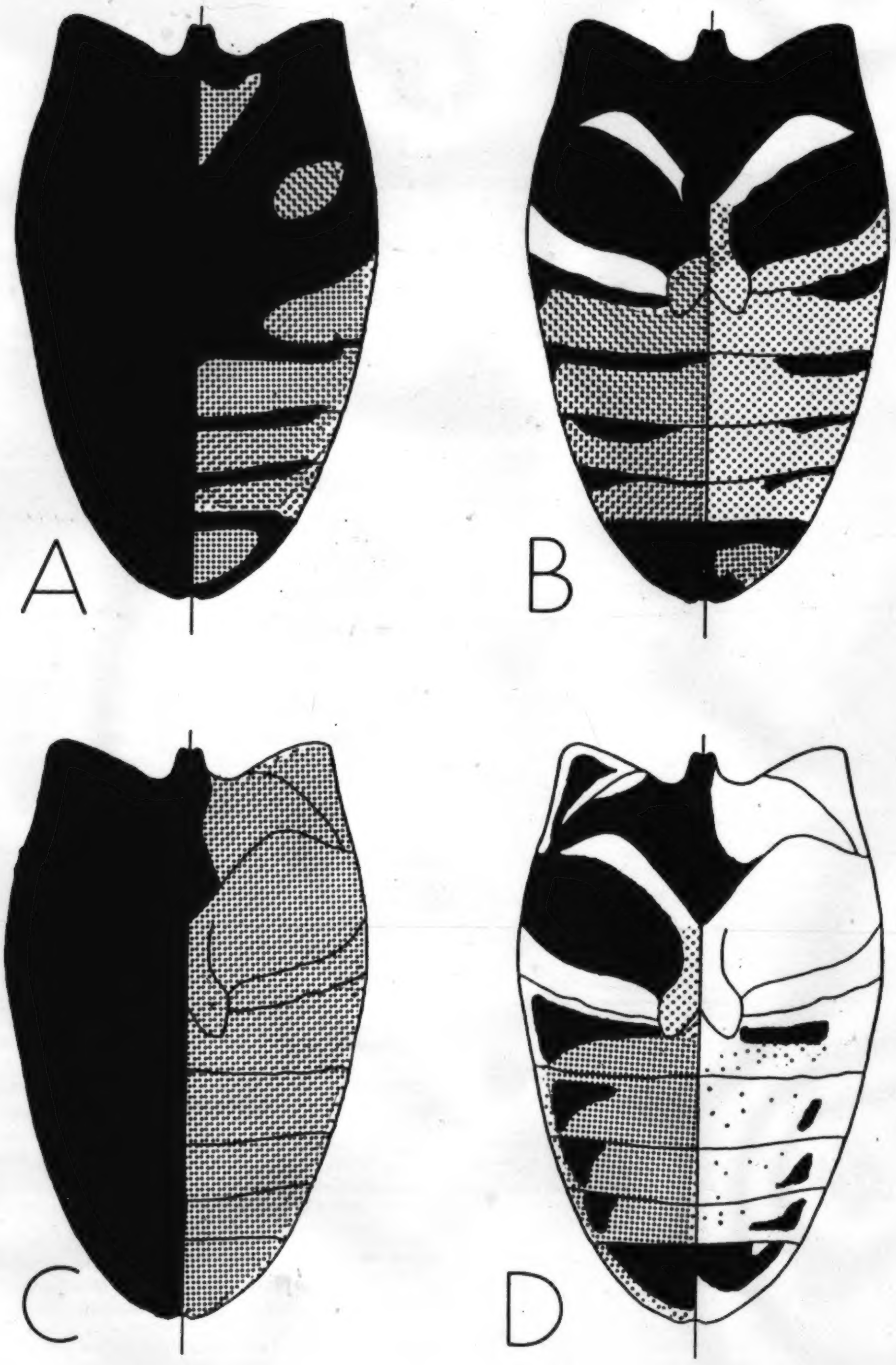

B

Figure 7. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. verticalis*, B) *D. harrisii*, C) *D. hybridus*, D) *D. marginicollis*.


A
B
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D

Figure 8. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. habilis*, B) *D. semisulcatus*, C) *D. sharpi*, D) *D. carolinus*.

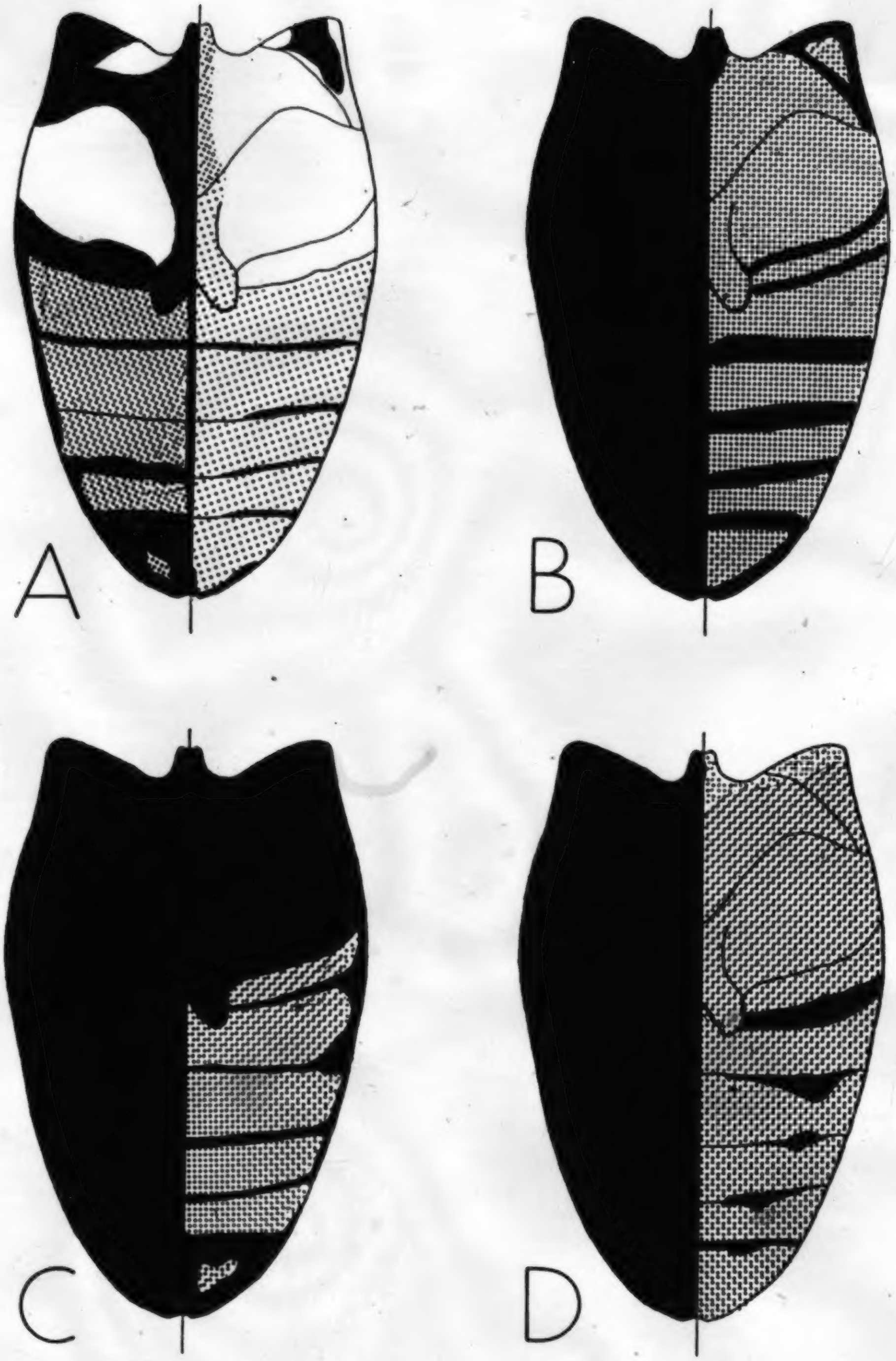
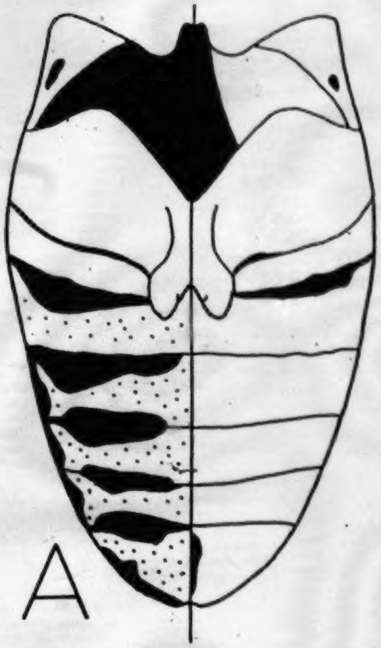
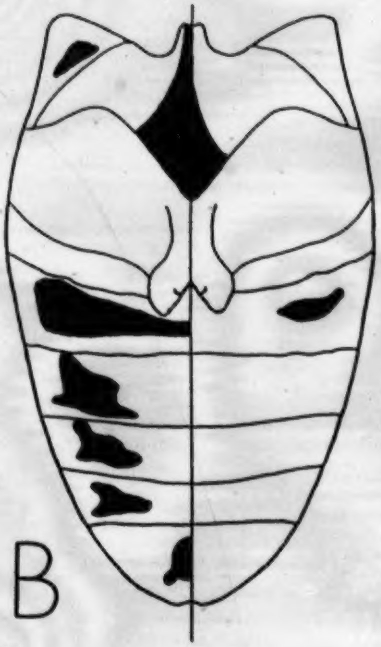

A
B
C
D

Figure 9. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. fasciventris*, B) *D. hatchi*, C) *D. cordieri*, D) *D. mutinensis*.



A



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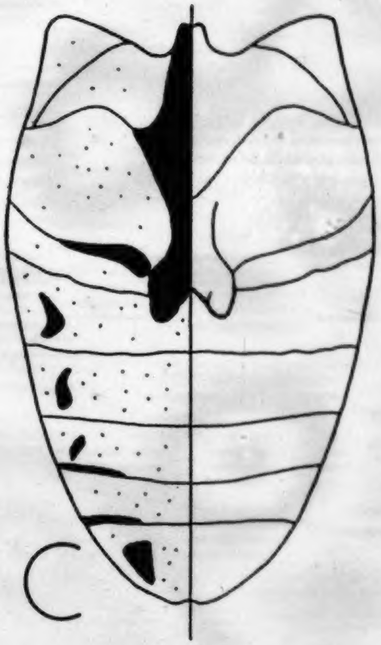

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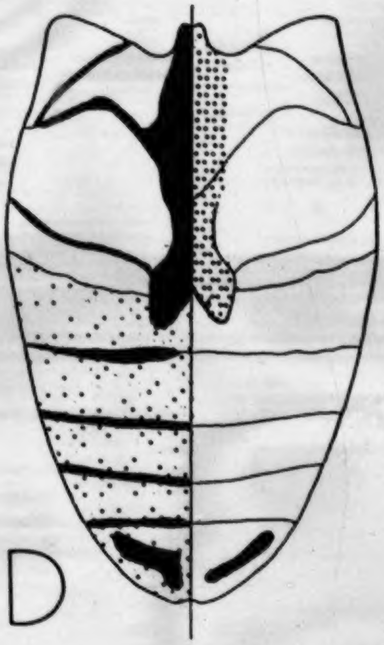
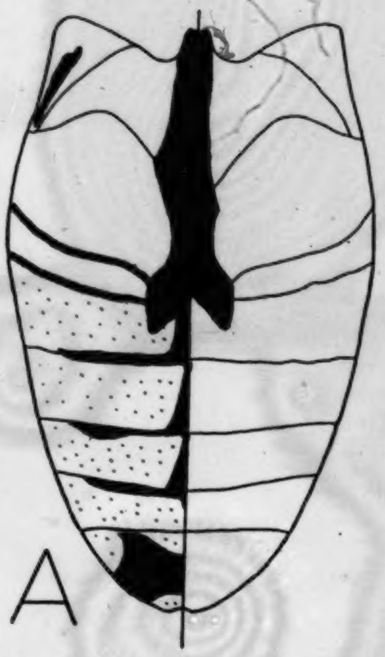
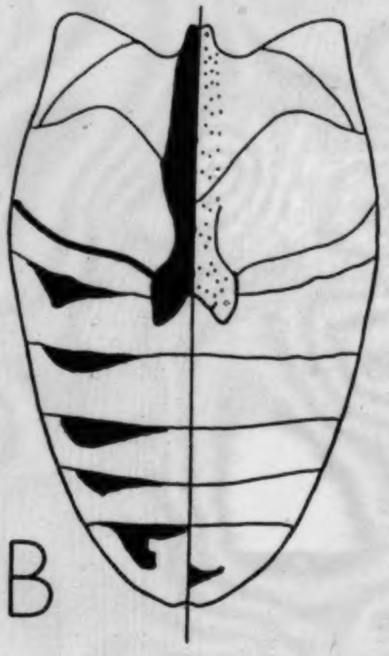


D

Figure 10. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species and subspecies of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. dimidiatus*, B) *D. pisanus*, C) *D. marginalis marginalis*, D) *D. marginalis czerskii*.



A



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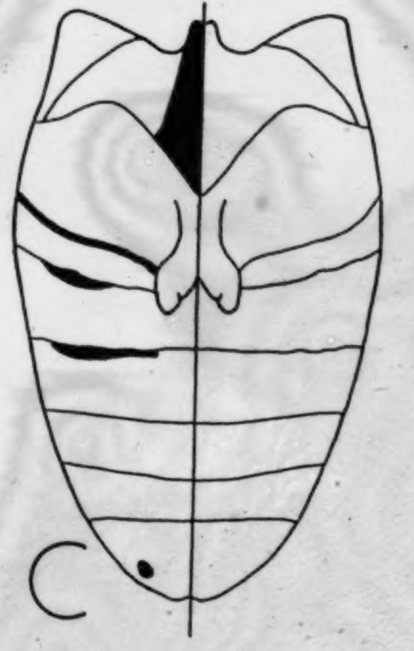

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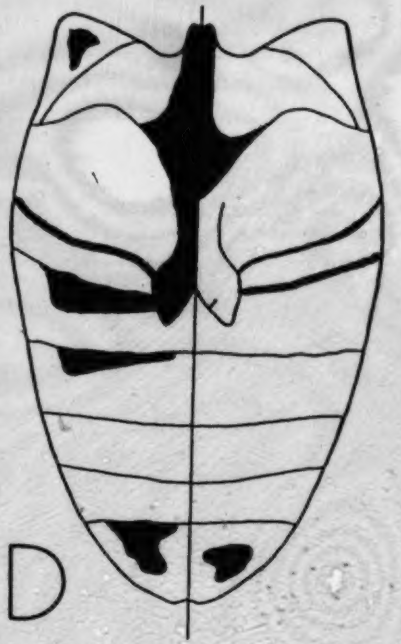


D

Figure 11. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. persicus*, B) *D. delictus*, C) *D. latissimus*, D) *D. circumcinctus*.

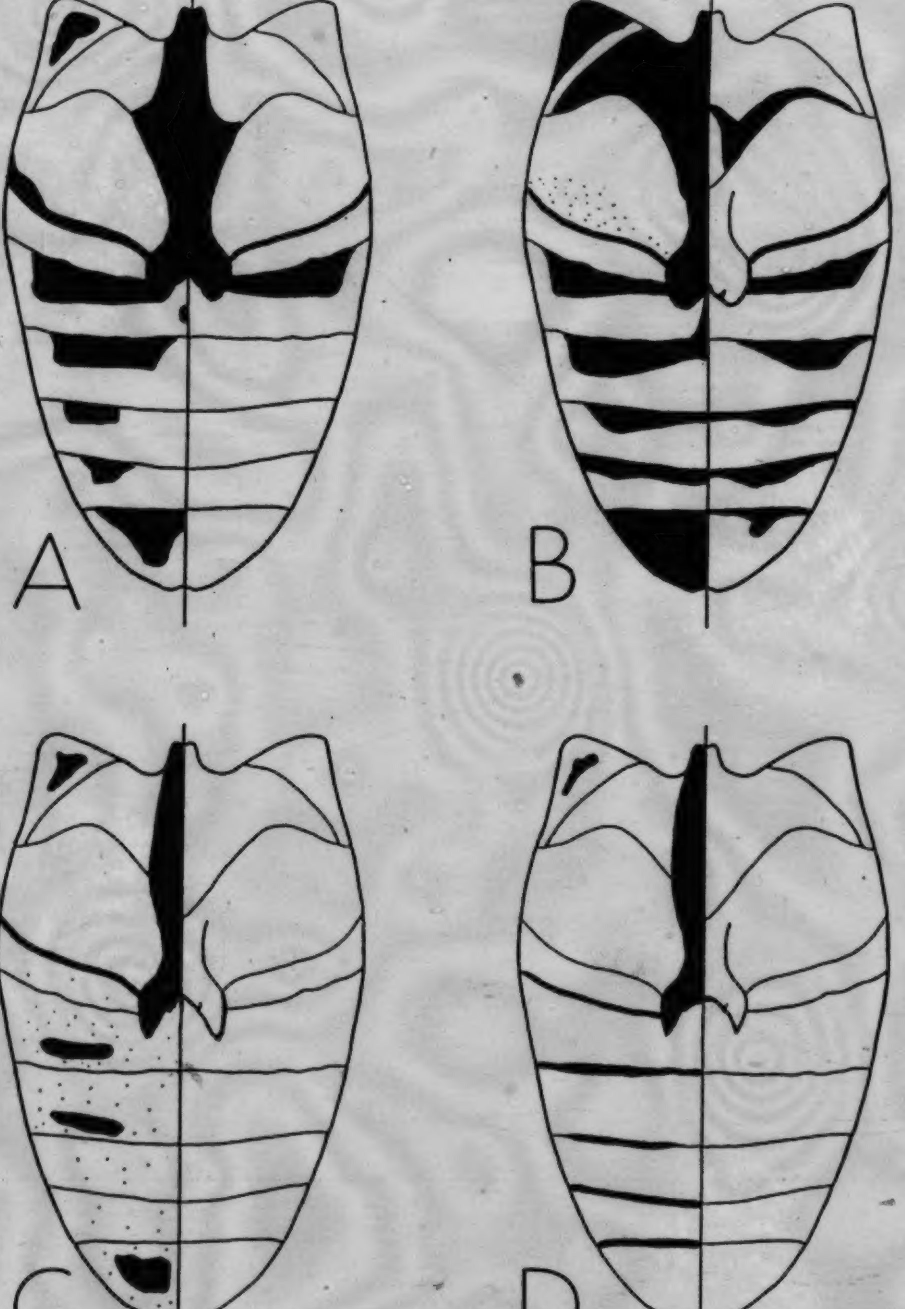

A
B
C
D

Figure 12. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species and subspecies of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. alaskanus*, B) *D. dauricus*, C) *D. lapponicus lapponicus*, D) *D. lapponicus disjunctus*.

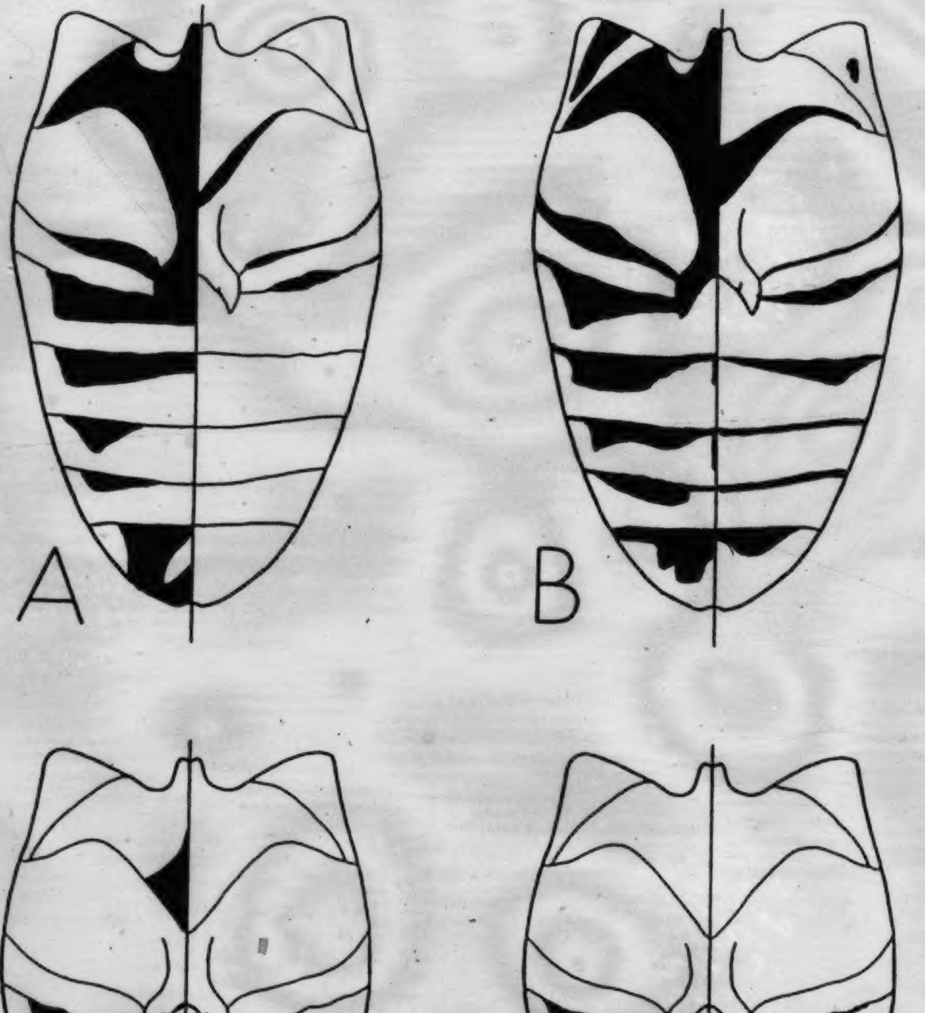
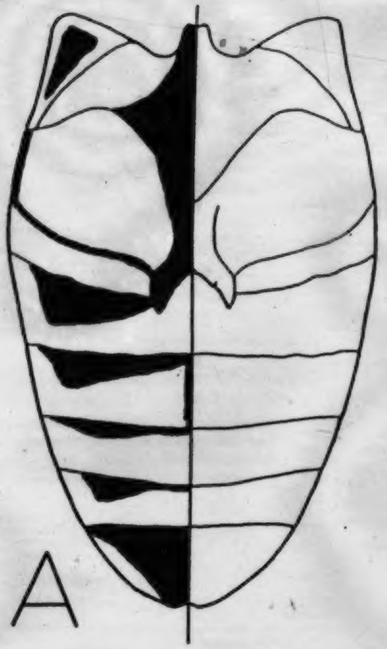
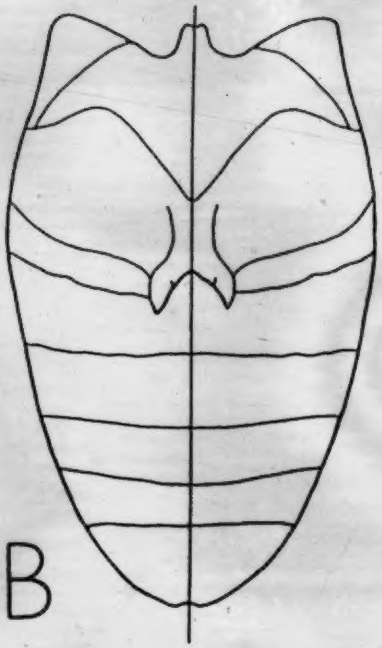

A
B
C
D

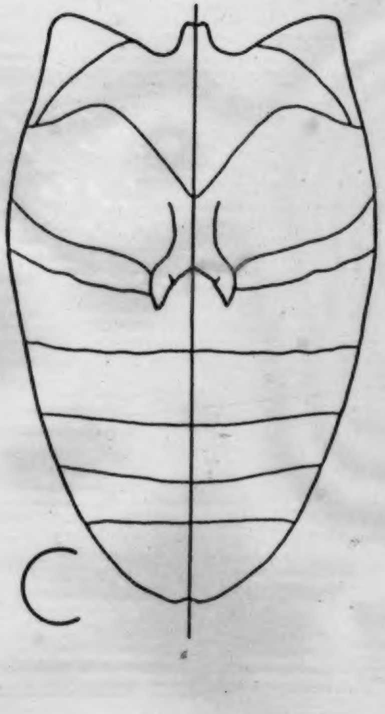
Figure 13. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* L. Darkest specimen on left, lightest on right. Black or piceous is represented as black on the figure, yellow by white, and red by stippling with more dense stippling indicating darker red. A) *D. circumflexus*, B) *D. thianshanicus*, C) *D. latro*, D) *D. sinensis*.



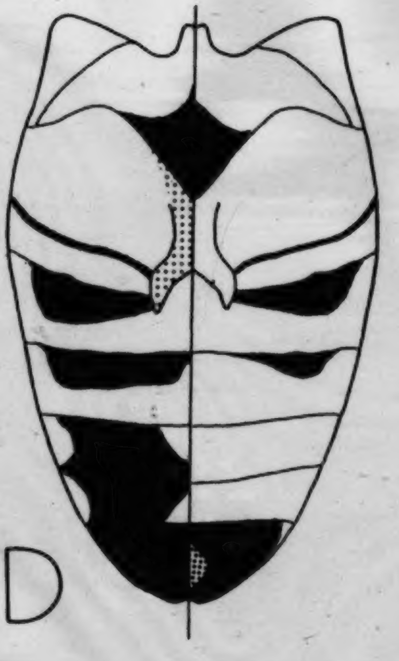
A



B



C



D

Figure 14. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. Scale bar is 1 mm. A) *D. verticalis*, B) *D. harrisii*, C) *D. hybridus*, D) *D. marginicollis*.

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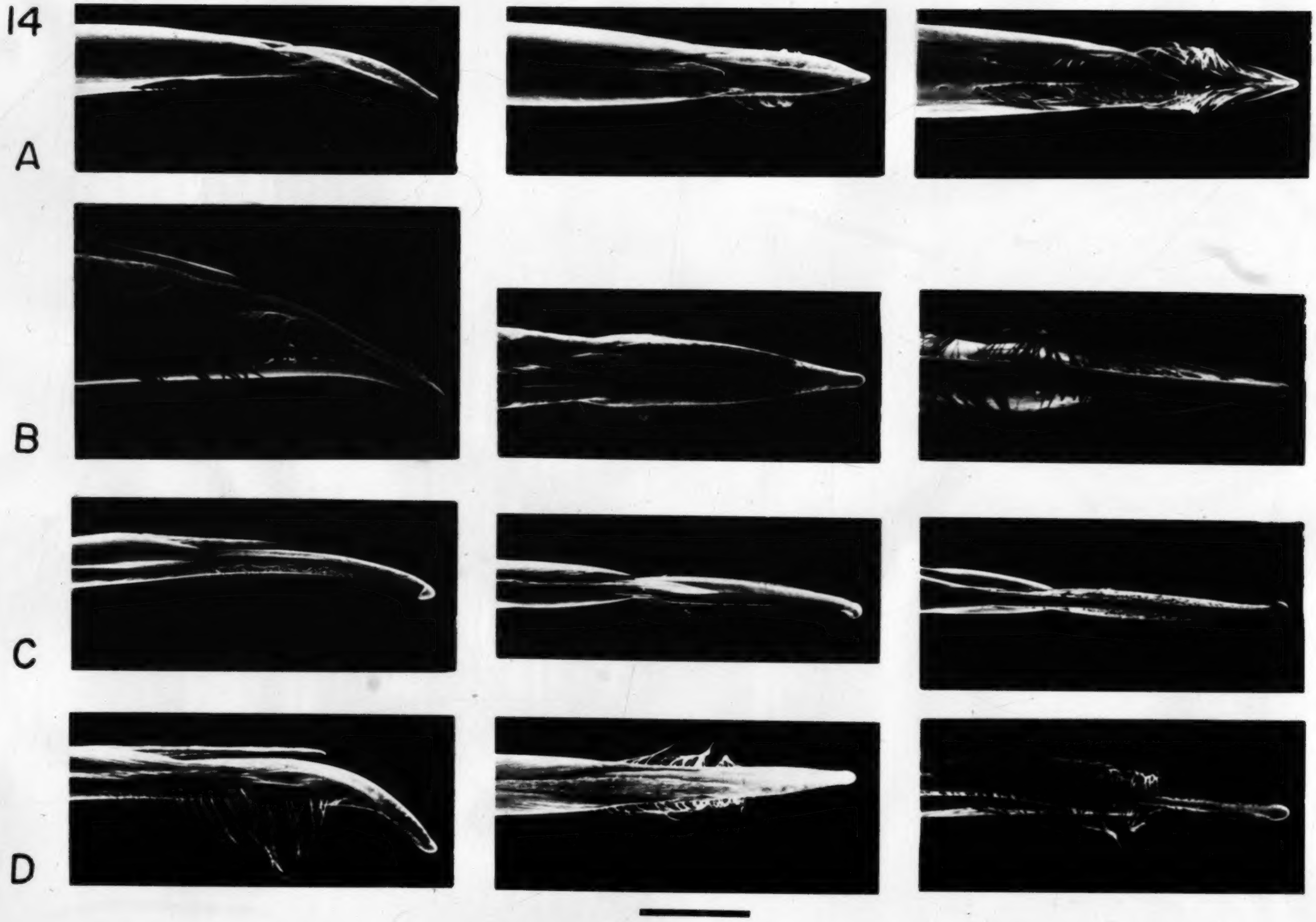


Figure 15. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. Scale bar is 1 mm. A) *D. habilis*, B) *D. semisulcatus*, C) *D. sharpi*, D) *D. carolinus*.

15

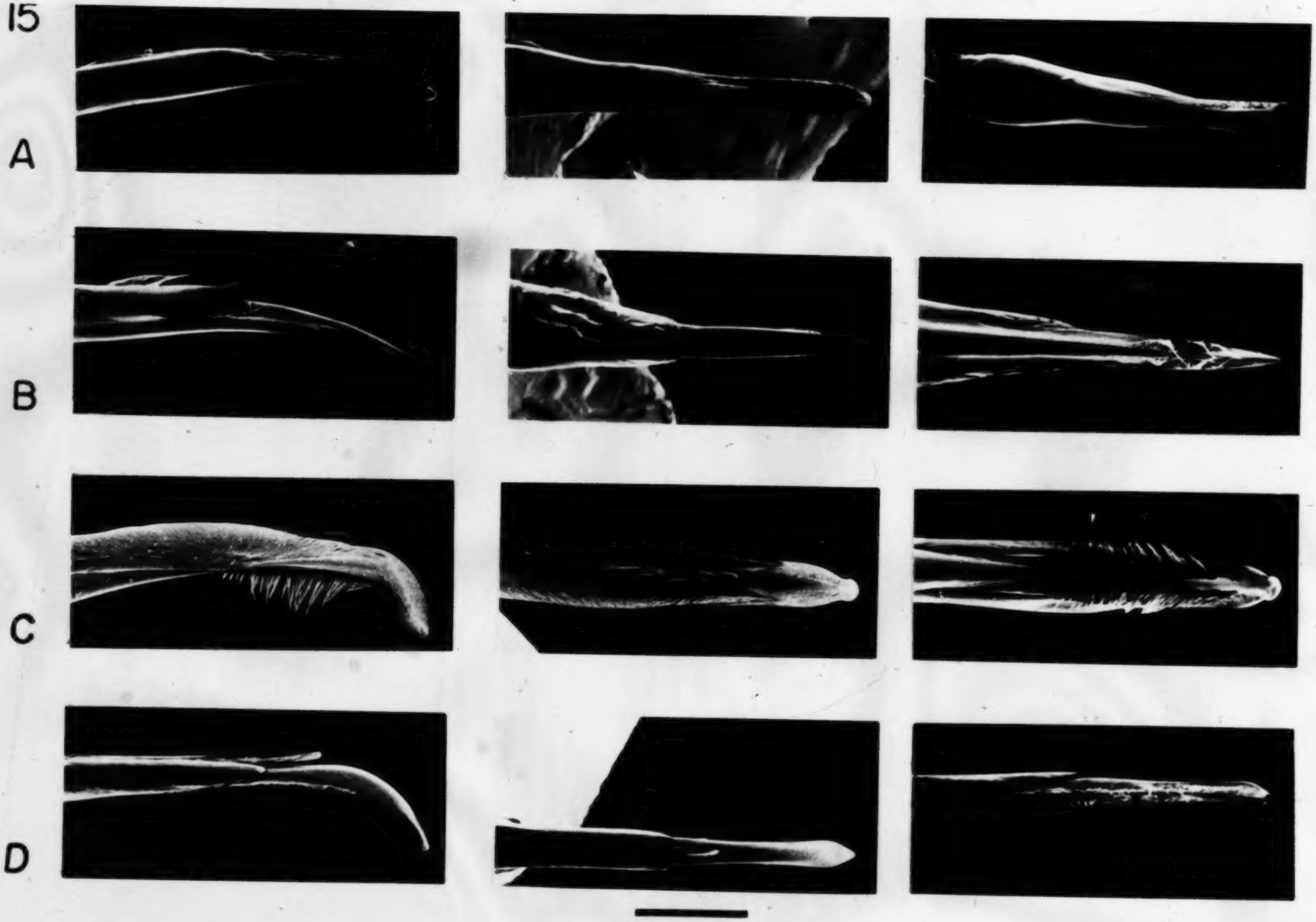


Figure 16. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. Scale bar is 1 mm. A) *D. fasciventris*, B) *D. hatchi*, C) *D. cordieri*, D) *D. mutinensis*.

16

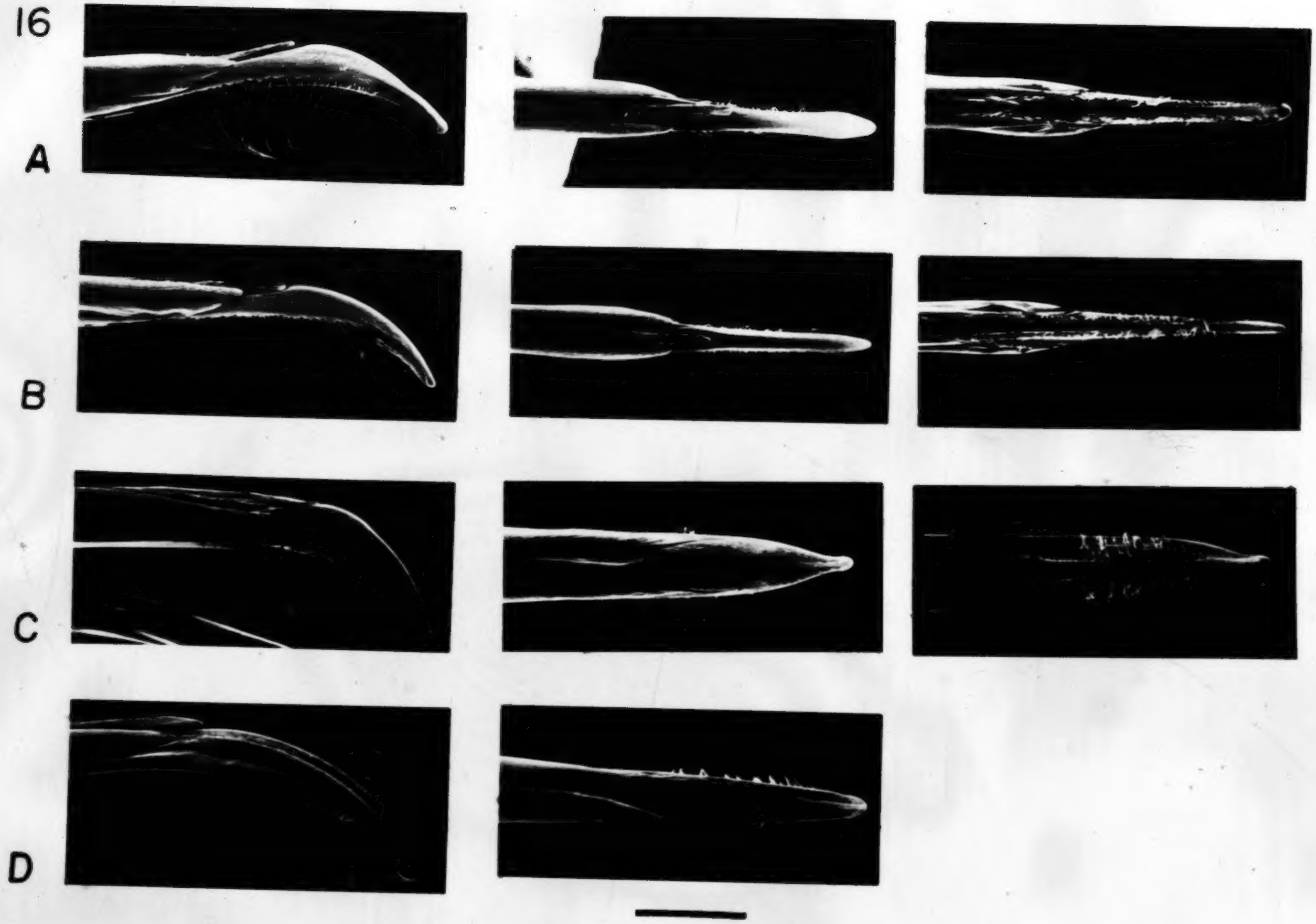


Figure 17. Scanning electron micrographs of apex of median lobe of males of species and subspecies of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. Scale bar is 1 mm. A) *D. dimidiatus*, B) *D. pisanus*, C) *D. marginalis marginalis*, D) *D. marginalis czerskii*.

17

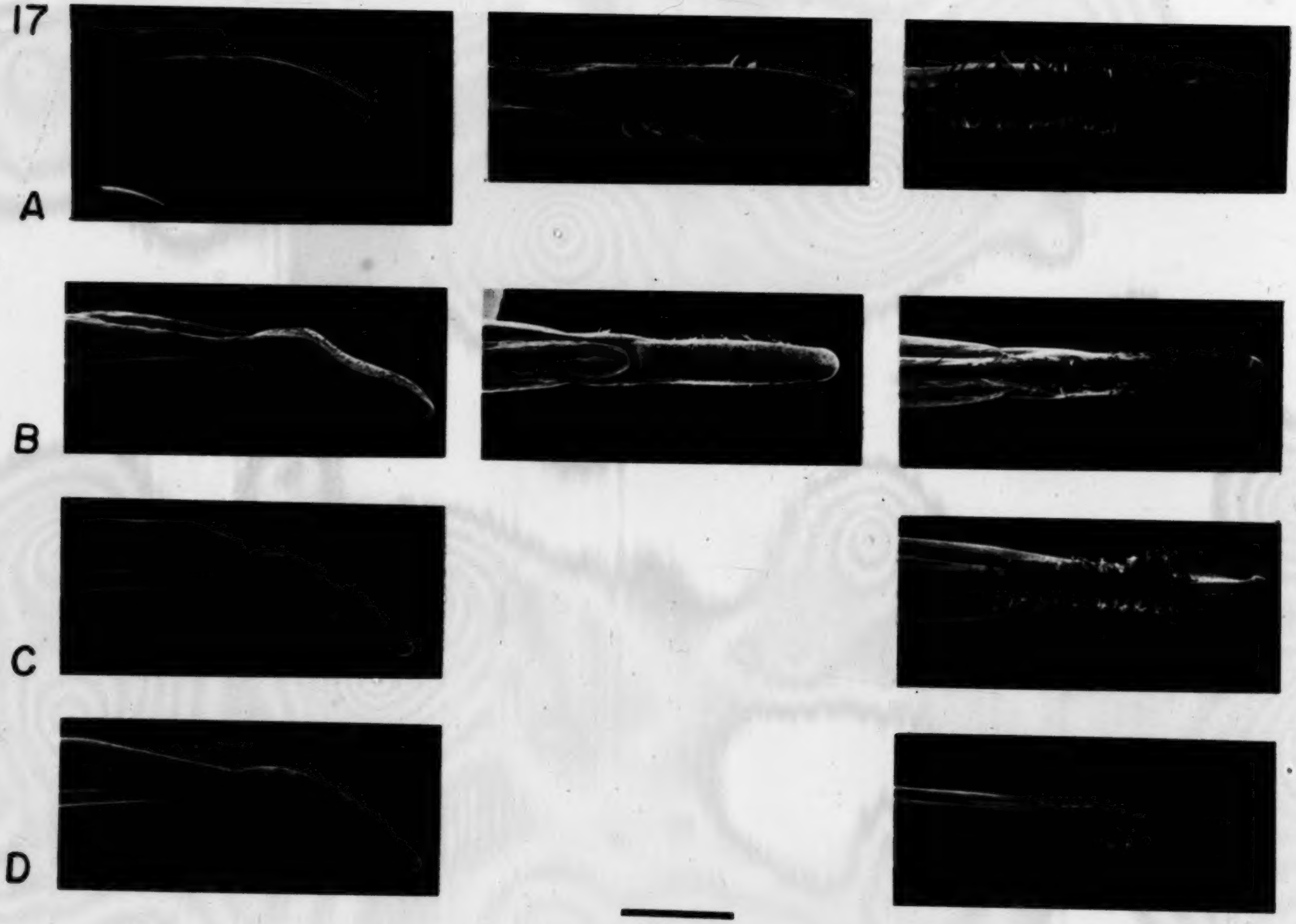


Figure 18. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. Scale bar is 1 mm. A) *D. persicus*, B) *D. delictus*, C) *D. latissimus*, D) *D. circumcinctus*, Palearctic specimen.

18

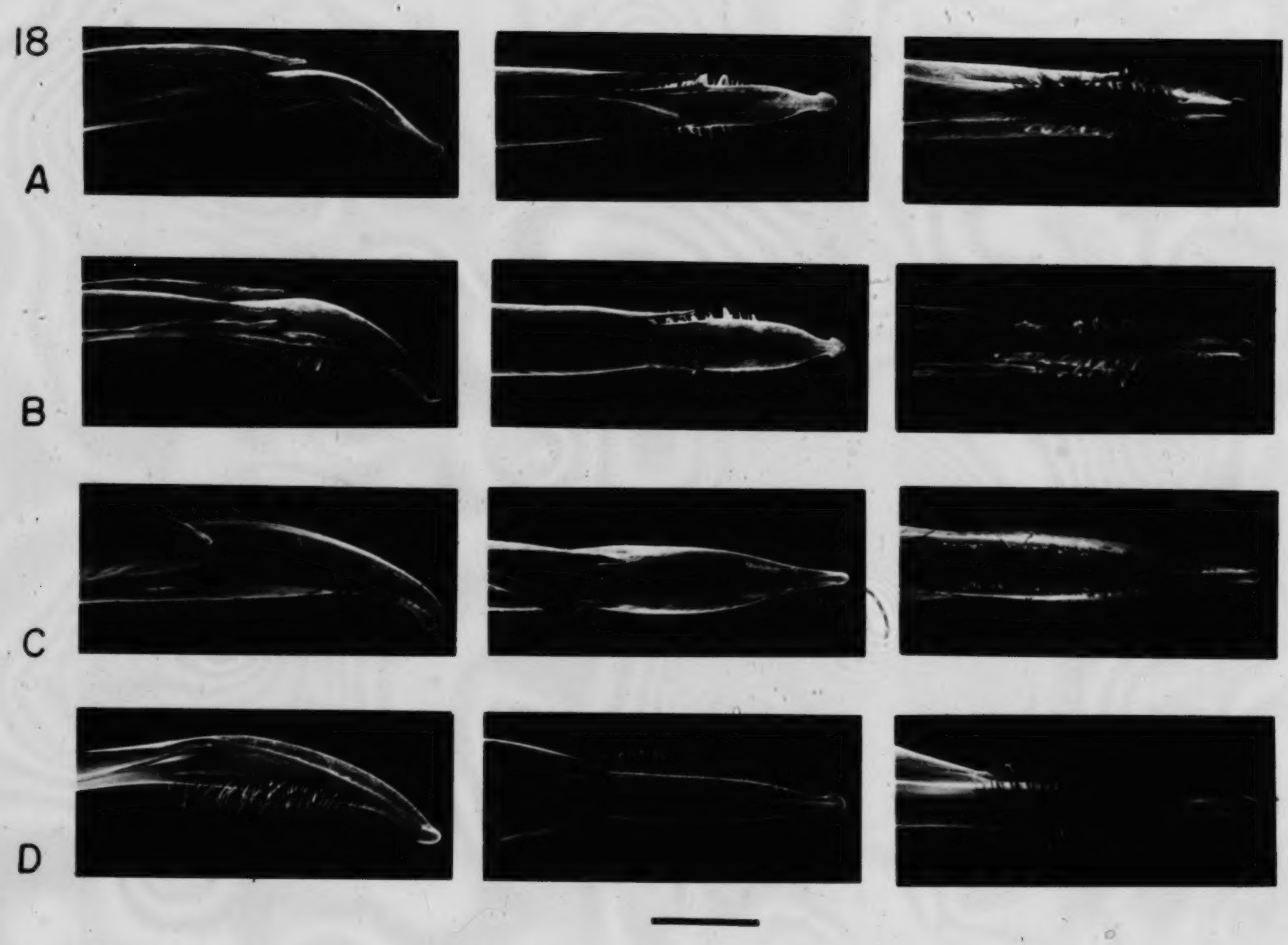


Figure 19. Scanning electron micrographs of apex of median lobe of males of species and subspecies of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. A) *D. circumcinctus*, Nearctic specimen, B) *D. alaskanus*, C) *D. dauricus*, D) *D. lapponicus lapponicus*. E) Underside of apical knob of median lobe of *D. lapponicus lapponicus*. Scale bar is 1 mm.

19

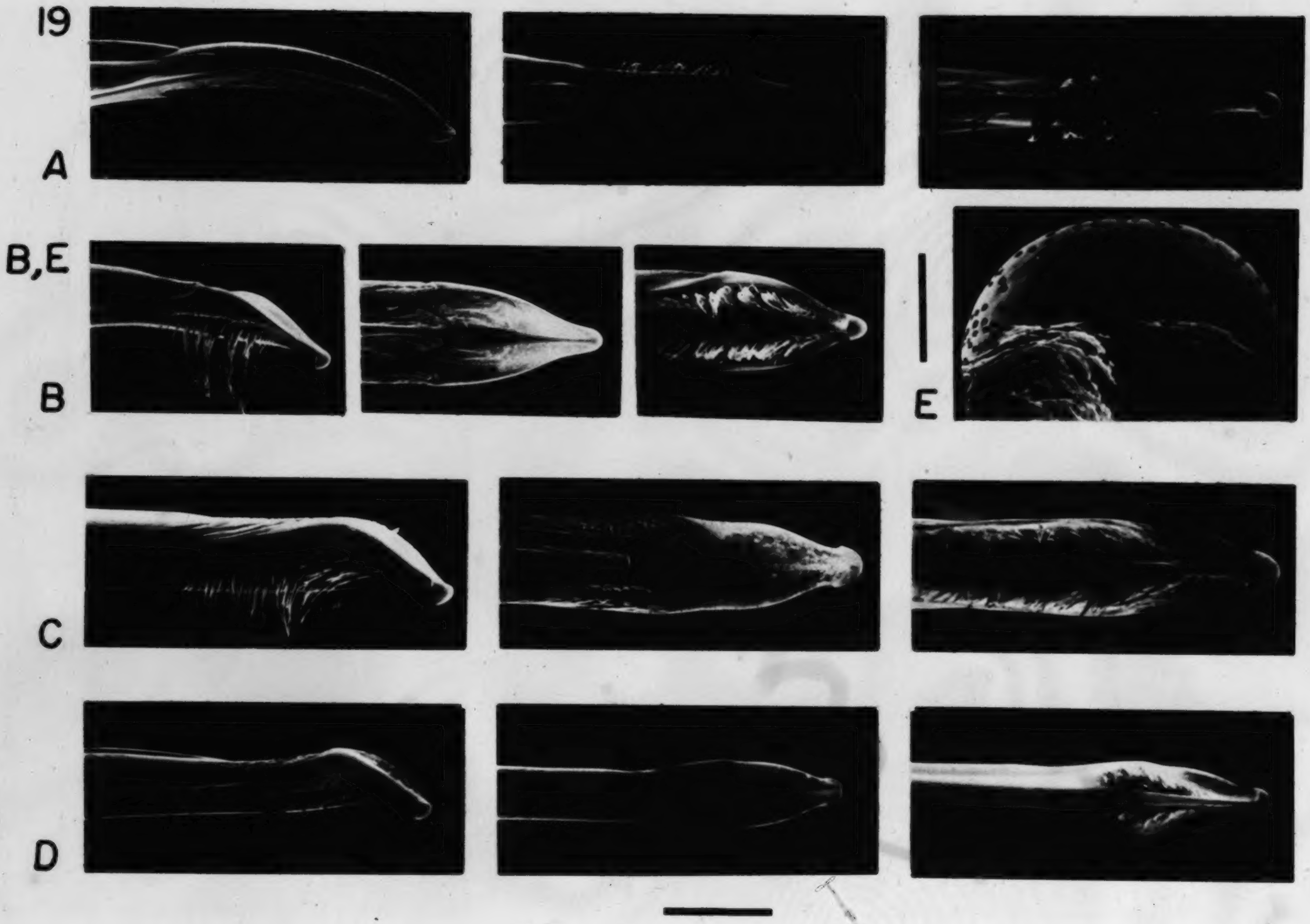


Figure 20. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* L. Lateral view on left, dorsal in centre, ventral on right. Scale bar is 1 mm. A) *D. circumflexus*, B) *D. thianshanicus*, C) *D. latro*, D) *D. sinensis*.

20

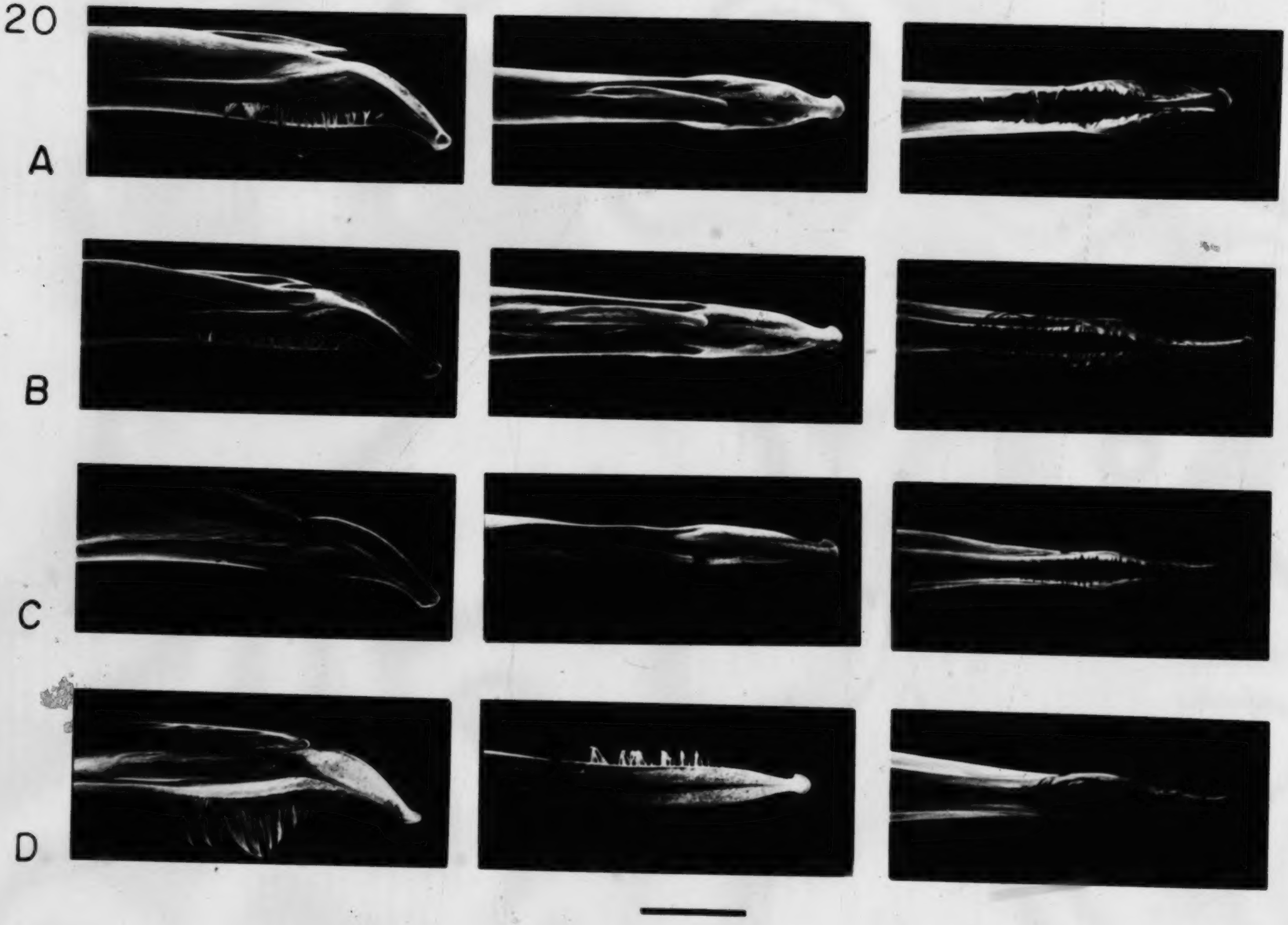
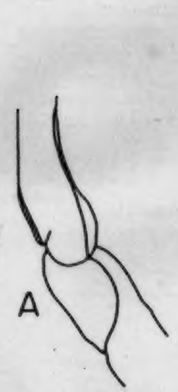


Figure 21. Left metacoxal process, trochanter and base of metafemur of species of *Dytiscus* L. A) *D. verticalis*, B) *D. harrisii*, C) *D. hybridus*, D) *D. marginicollis*, E) *D. habilis*, F) *D. semisulcatus*, G) *D. sharpi*, H) *D. carolinus*, I) *D. fasciventris*, J) *D. hatchi*, K) *D. cordieri*, L) *D. mutinensis*, M) *D. dimidiatus*, N) *D. pisanus*.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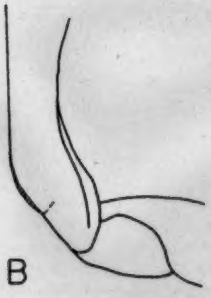
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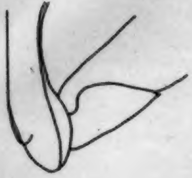
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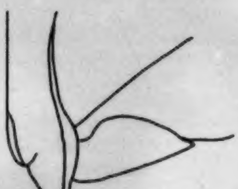
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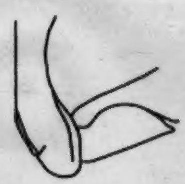
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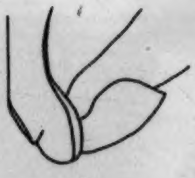
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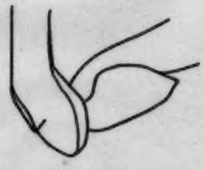
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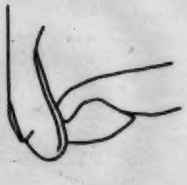
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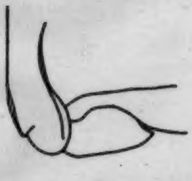
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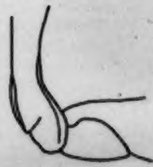
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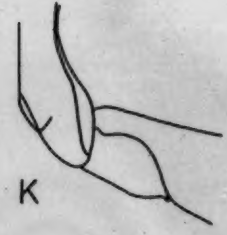
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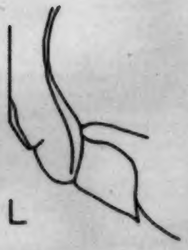
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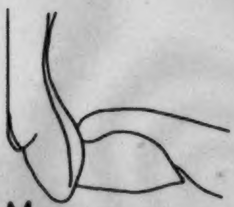
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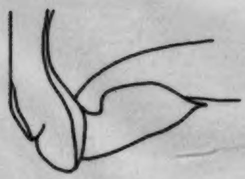
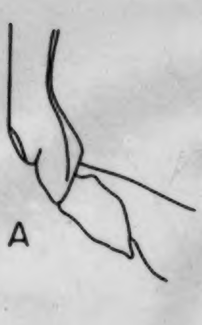
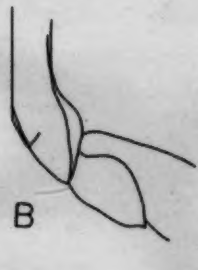
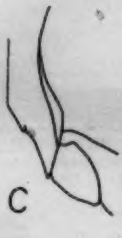

N

Figure 22. Left metacoxal process, trochanter and base of metafemur of species and subspecies of *Dytiscus* L.
A) *D. marginalis marginalis*, B) *D. marginalis czerskii*,
C) *D. persicus*, D) *D. delictus*, E) *D. latissimus*,
F) *D. circumcinctus*, G) *D. alaskanus*, H) *D. dauricus*,
I) *D. lapponicus lapponicus*, J) *D. lapponicus disjunctus*,
K) *D. circumflexus*, L) *D. thianshanicus*, M) *D. latro*,
N) *D. sinensis*.


A


B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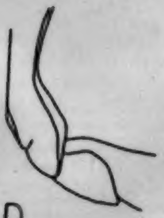
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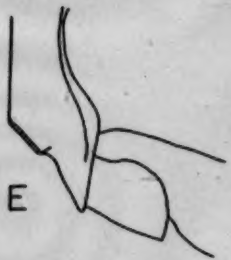
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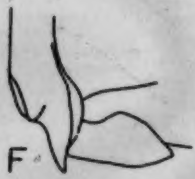
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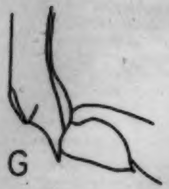
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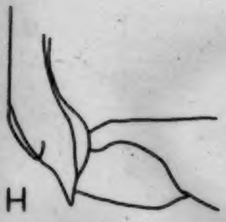
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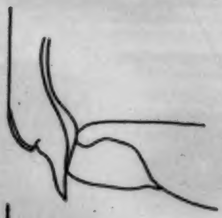
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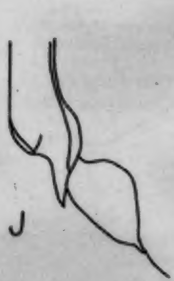
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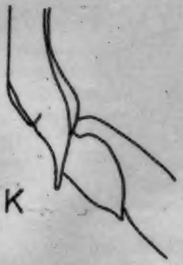
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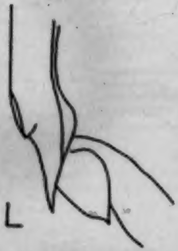
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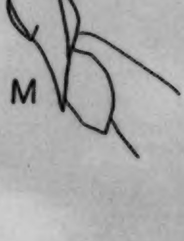
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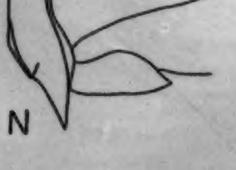

N

Figure 23. Structural features of species of *Dytiscus* L. A) Frontal view of head of *D. harrisii*. B) Frontal view of head of *D. cordieri*. C) Protarsomere IV and V plus claws of male of *D. hatchi*. D) Protarsomere IV and V plus claws of male of *D. fasciventris*. E) Mesotarsomere IV and V plus claws of female of *D. hatchi*. F) Mesotarsomere IV and V plus claws of female of *D. fasciventris*. G) Protarsomere IV and V plus claws of male of *D. mutinensis*. H) Protarsomere IV and V plus claws of male of *D. dimidiatus*. I) Mesotarsomere IV and V plus claws of female of *D. pisanus*. J) Mesotarsomere IV and V plus claws of female of *D. delictus*.

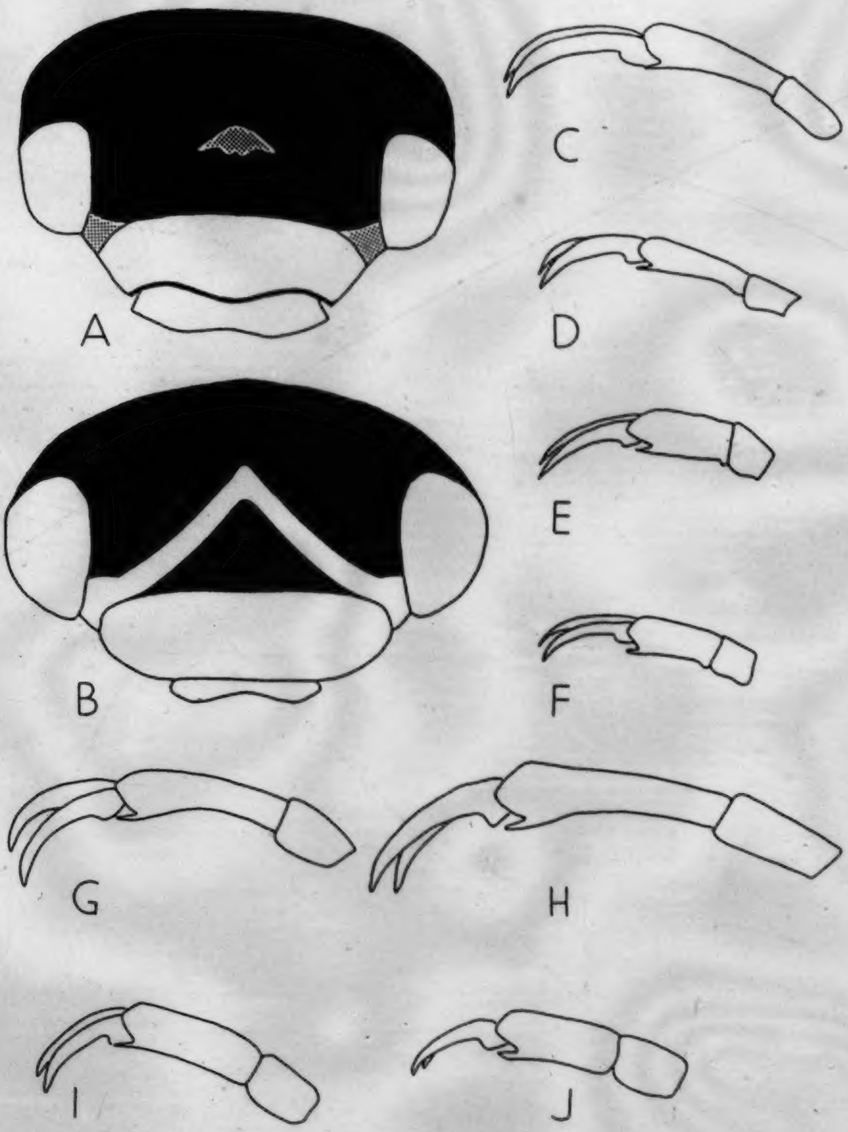

A
B
C
D
E
F
G
H
I
J

Figure 24. Known distribution as represented by locality information for species of *Dytiscus* L. A) *D. verticalis*, B) *D. harrisii*, C) *D. hybridus*, D) *D. marginicollis* (•) and *D. habilis* (×).

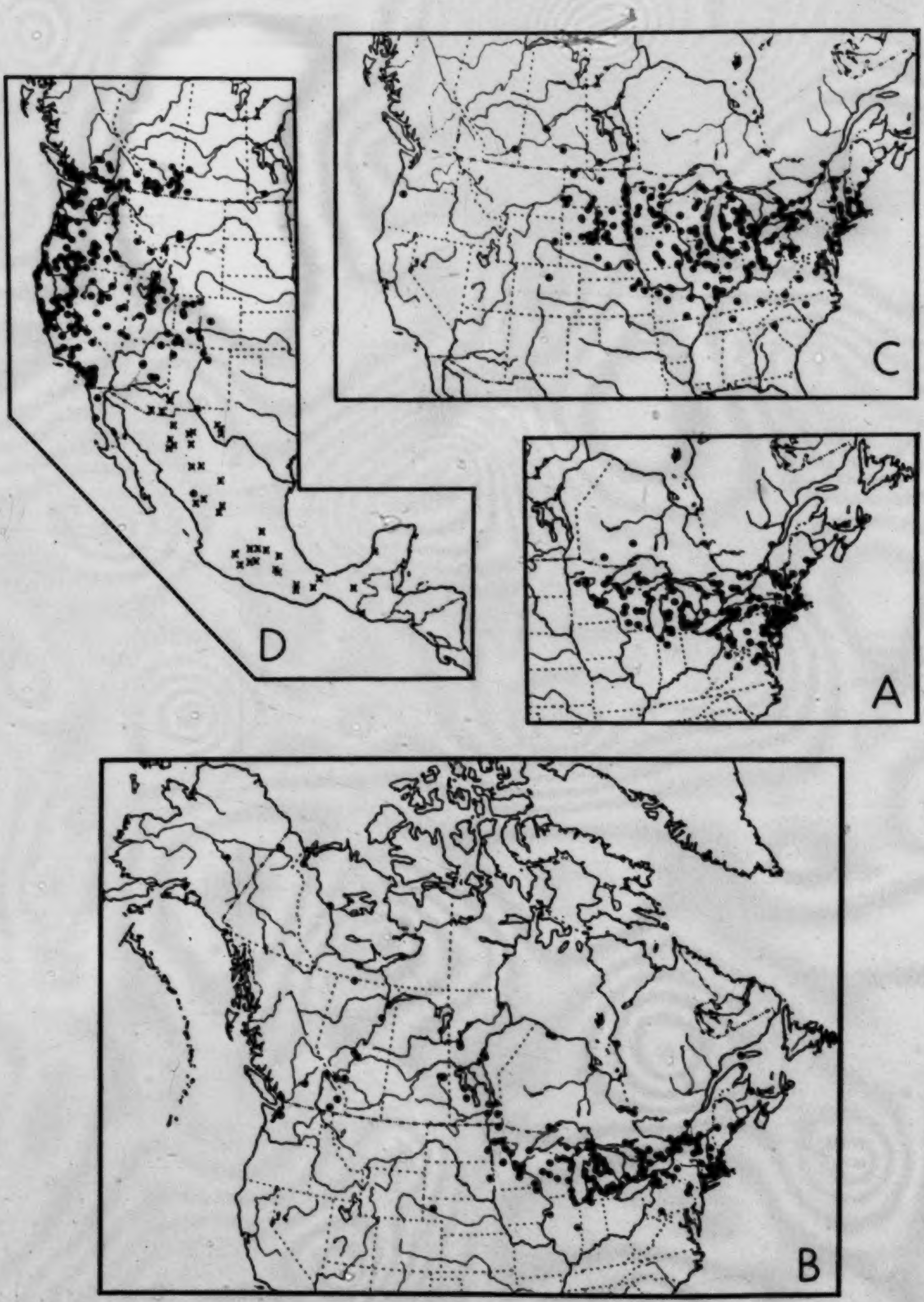

D
C
A
B

Figure 25. Known distribution as represented by locality information for species of *Dytiscus* L. A) *D. semisulcatus*, B) *D. sharpi*, C) *D. carolinus*, D) *D. fasciventris*, E) *D. hatchi*,

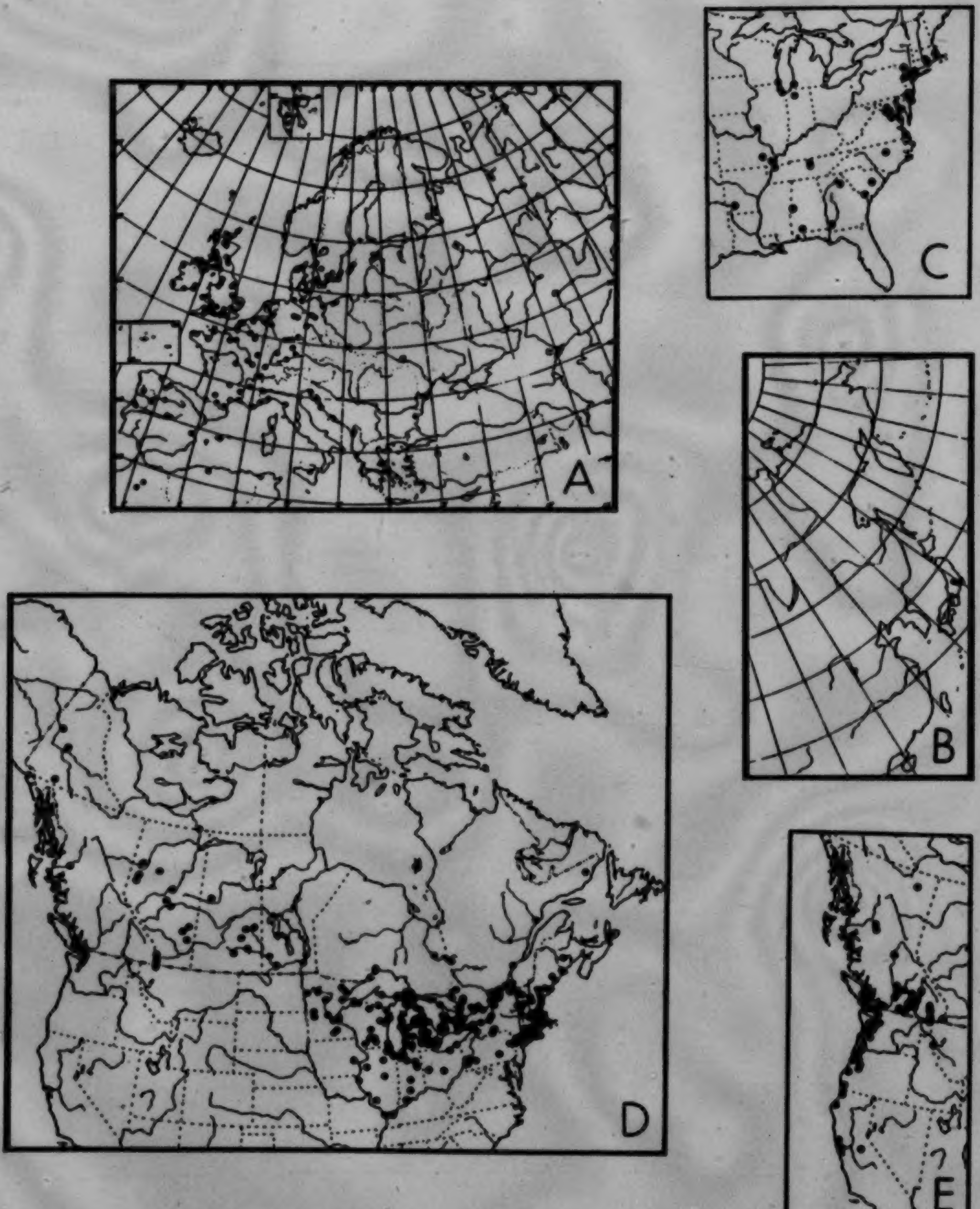
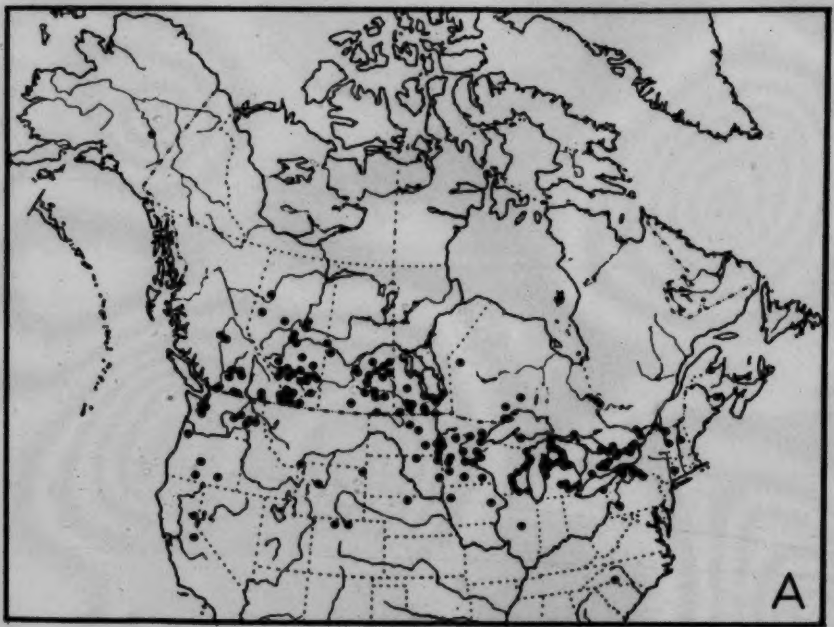
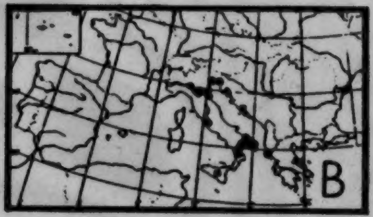
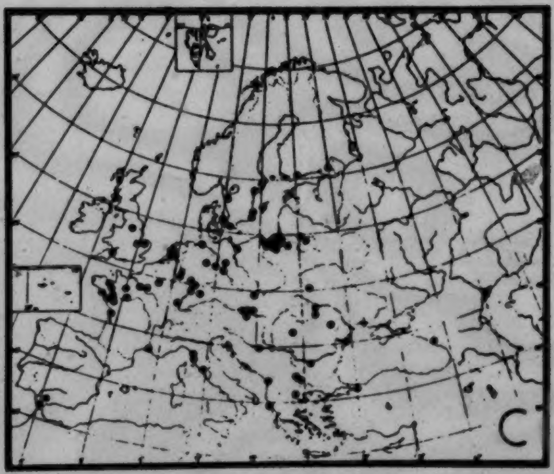

A
C
B
D
E

Figure 26. Known distribution as represented by locality information for species of *Dytiscus* L. A) *D. cordieri*, B) *D. mutinensis*, C) *D. dimidiatus*, D) *D. pisanus*.


A


B


C

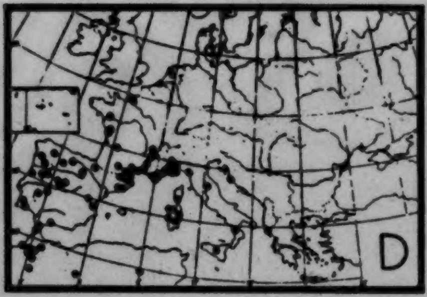

D

Figure 27. Known distribution as represented by locality information for species and subspecies of *Dytiscus* L. A) *D. marginalis marginalis* (filled and open circles) and *D. marginalis czerskii* (triangles), B) *D. persicus*, C) *D. delictus*, D) *D. latissimus*, E) *D. circumcinctus*, in Palearctic region, F) *D. circumcinctus*, in Nearctic region.

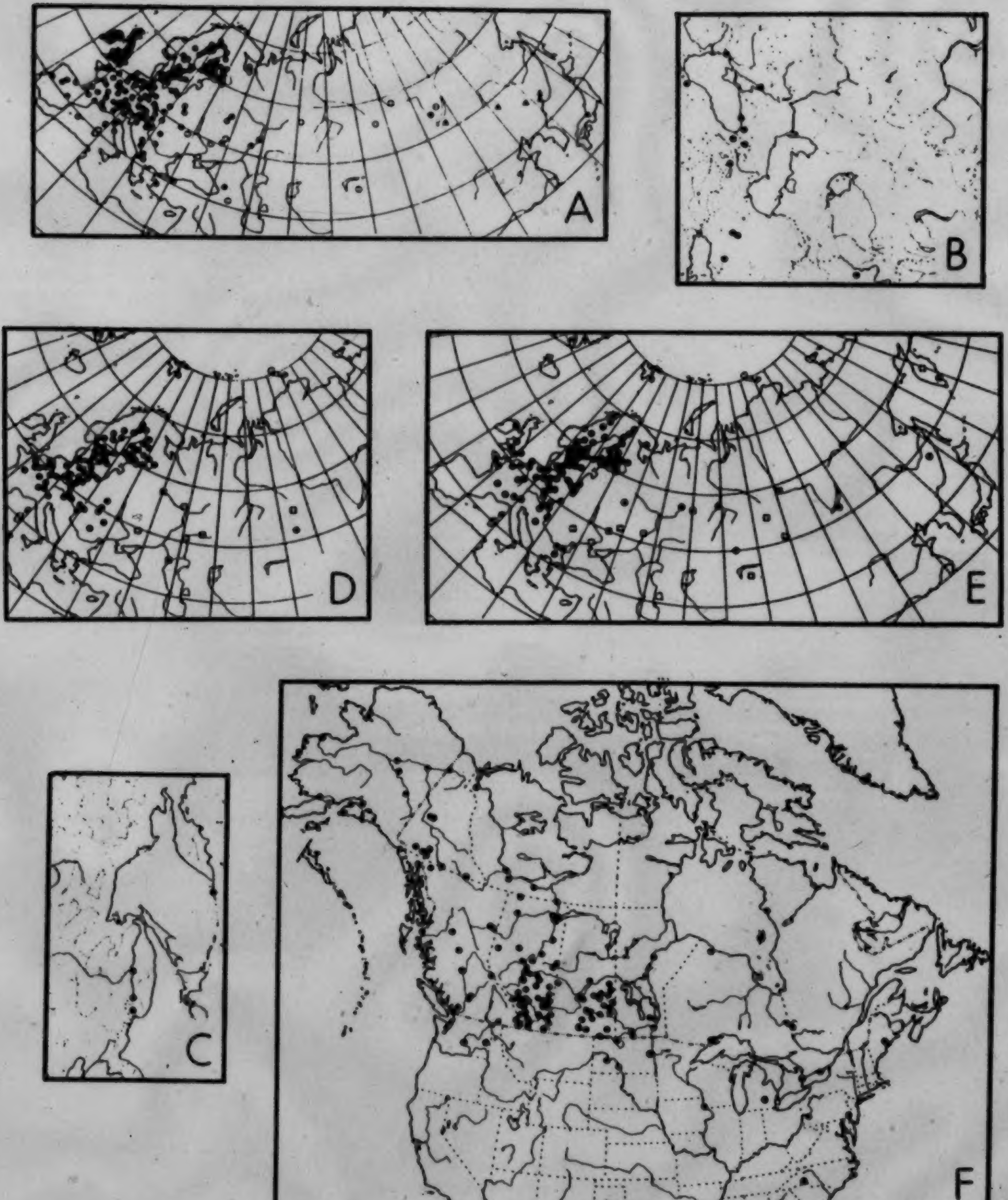

A
B
D
E
C
F

Figure 28. Known distribution as represented by locality information for species and subspecies of *Dytiscus* L. A) *D. alaskanus*, B) *D. dauricus*, in Palearctic region, C) *D. dauricus*, in Nearctic region, D) *D. lapponicus lapponicus* (filled circles and open boxes) and *D. lapponicus disjunctus* (triangles).

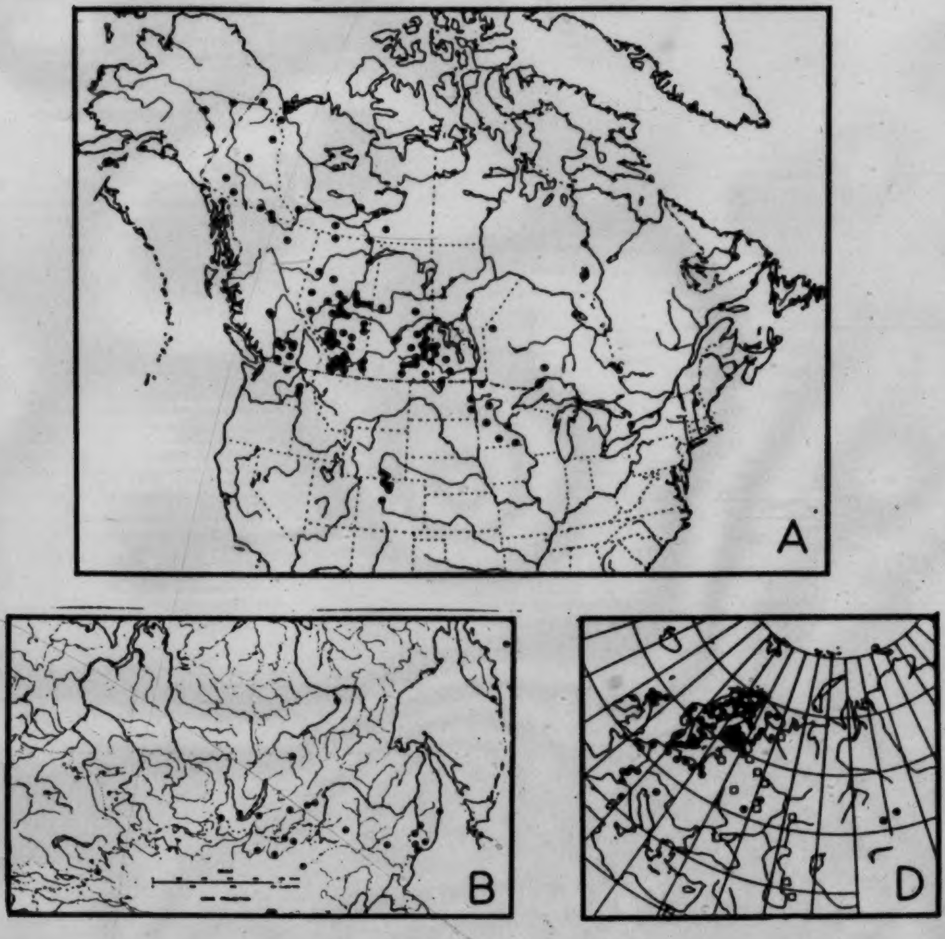
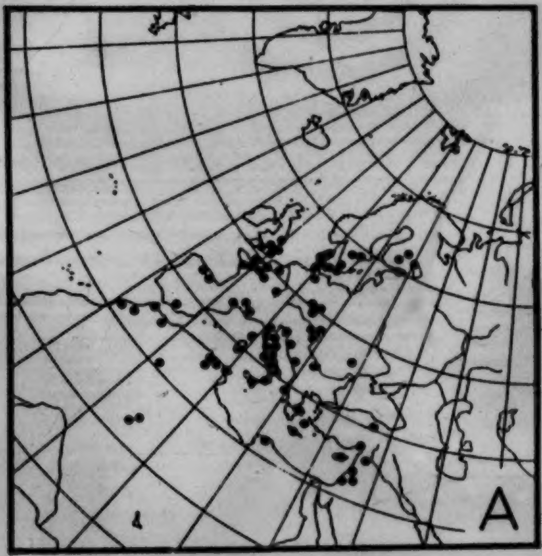
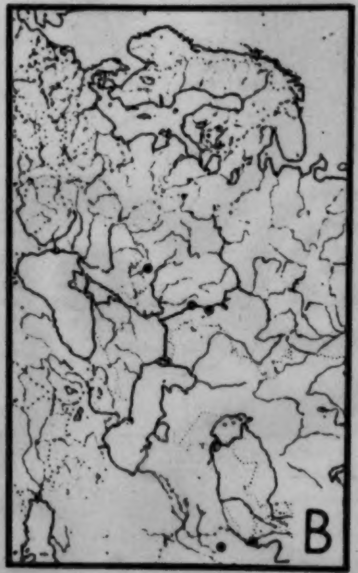
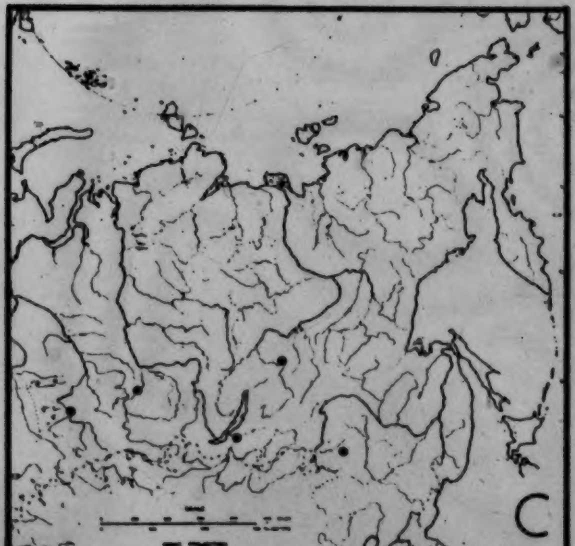

A
B
D
C

Figure 29. Known distribution as represented by locality information for species of *Dytiscus* L. A) *D. circumflexus*, B) *D. thianshanicus*, C) *D. latro*, D) *D. sinensis*.


A


B


C

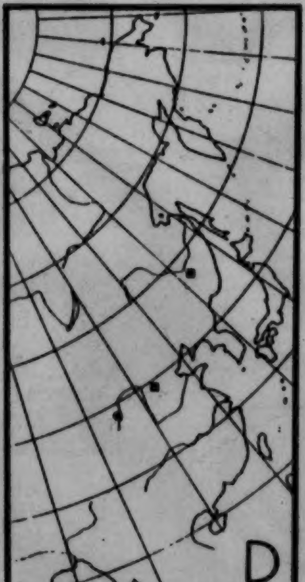

D

Figure 30. Phylogeny of species of *Dytiscus* L. Filled circles signify apomorphic states and open circles plesiomorphic states. Species groups of *Dytiscus* are indicated by vertical lines with a check mark denoting nominate species. Filled ellipses indicate distribution in Palearctic or Nearctic regions

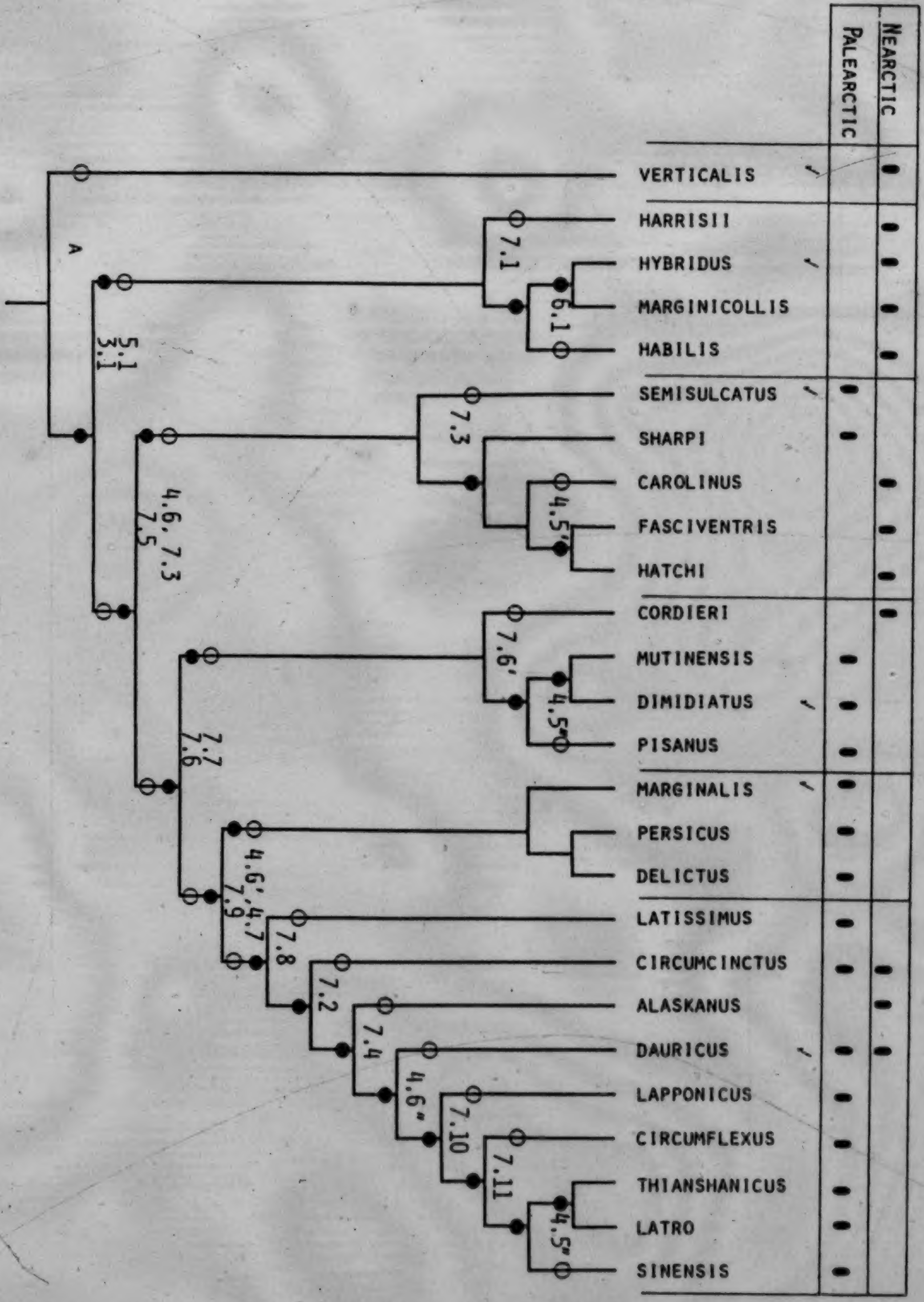
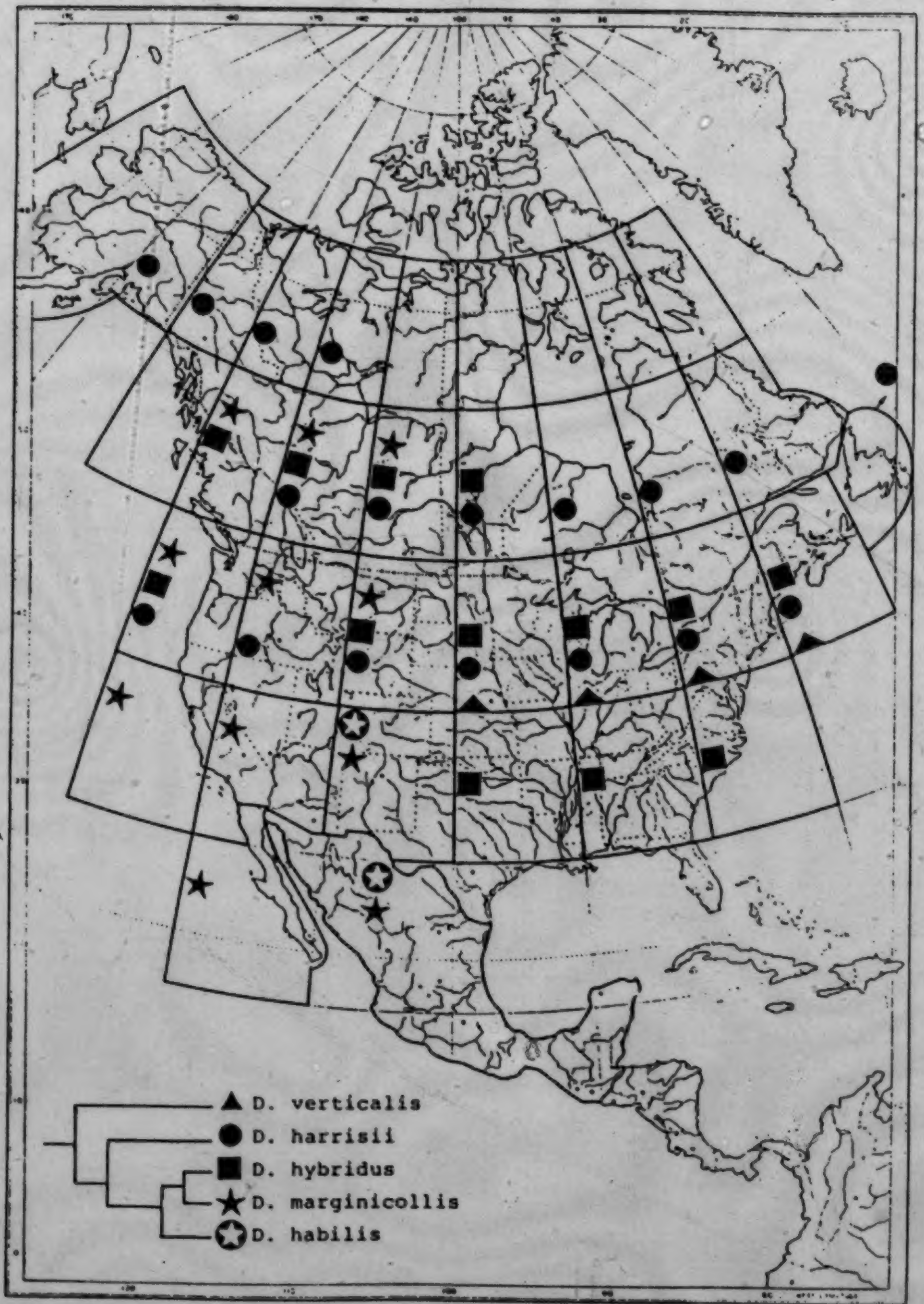

NEARCTIC
PALEARCTIC
VERTICALIS
HARRISII
HYBRIDUS
MARGINICOLLIS
HABILIS
SEMISULCATUS
SHARPI
CAROLINUS
FASCIVENTRIS
HATCHI
CORDIERI
MUTINENSIS
DIMIDIATUS
PISANUS
MARGINALIS
PERSICUS
DELICTUS
LATISSIMUS
CIRCUMCINCTUS
ALASKANUS
DAURICUS
LAPPONICUS
CIRCUMFLEXUS
THIANSHANICUS
LATRO
SINENSIS
A
5.1
3.1
7.1
6.1
4.6, 7.3
7.5
7.3
4.5'
7.6'
4.5'
7.7
7.6
4.6', 4.7
7.9
7.8
7.2
7.4
4.6"
7.10
7.11
4.5"

Figure 31. Chorological and phylogenetic relationships of species of the *D. verticalis*- and *D. hybridus*-groups. Generalized from Figures 24 and 30. Occurrence of taxa in areas delimited by darker lines is indicated by symbol in legend.


▲ D. verticalis
● D. harrisii
■ D. hybridus
★ D. marginicollis
✪ D. habilis

Vita

I was born in Guelph, Ontario on 14 May, 1950, and grew up in the rural village of Limehouse (now Halton Mills), Ontario. After public school education, I achieved Senior Matriculation (Grade 13) from Acton District High School. My university education began at the University of Guelph. Prior to this time, I can recall having no specific interest in insects. However, during my time at Guelph, my interest in insects in general, and in the discipline of taxonomy in particular was piqued and encourage by Dr. D.H. Pengelly. I completed my B.Sc.Agr. in 1974 and began an M.Sc. program under Dr. Pengelly at that time. The subject of this thesis was a revision fo Nearctic species of *Hydaticus* Leach (Coleoptera: Dytiscidae). This project was completed in 1976 and in the same year, I began a Ph.D. program at the University of Alberta. On 18 January, 1982, I was hired at Assistant Professor level by the University of Manitoba to teach and conduct research in the Department of Entomology.

On 13 May, 1972, I married Marsha Lynn McKenzie, and we now have two children: Amy Rebecca, born 30 October, 1979, in Edmonton, and Katherine Anne, born 28 October, 1982, in Winnipeg.